The evolutionary history of Mimosa (Leguminosae): toward a phylogeny of the sensitive plants

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Abstract: Premise of the study: Large genera provide remarkable opportunities to investigate patterns of morphological evolution and historical biogeography in plants. A molecular phylogeny of the species-rich and morphologically and ecologically diverse genus Mimosa was generated to evaluate its infrageneric classification, reconstruct the evolution of a set of morphological characters, and establish the relationships of Old World species to the rest of the genus. • Methods: We used trnD-trnT plastid sequences for 259 species of Mimosa (ca. 50% of the total) to reconstruct the phylogeny of the genus. Six morphological characters (petiolar nectary, inflorescence type, number of stamens, number of petals, pollen type, and seismonasty) were optimized onto the molecular tree. • Key results: Mimosa was recovered as a monophyletic clade nested within the Piptadenia group and includes the former members of Schrankia, corroborating transfer of that genus to Mimosa. Although we found good support for several infrageneric groups, only one section (Mimadenia) was recovered as monophyletic. All but one of the morphological characters analyzed showed high levels of homoplasy. High levels of geographic structure were found, with species from the same area tending to group together in the phylogeny. Old World species of Mimosa form a monophyletic clade deeply nested within New World groups, indicating recent (6-10 Ma) long-distance dispersal. • Conclusions: Although based on a single plastid region, our results establish a preliminary phylogenetic framework for Mimosa that can be used to infer patterns of morphological evolution and relationships and which provides pointers toward a revised infrageneric classification.

DOI: https://doi.org/10.3732/ajb.1000520

American Journal of Botany

American Journal of Botany 98(7): 1201–1221. 2011.

The evolutionary history of *Mimosa* (Leguminosae): Toward a phylogeny of the sensitive plants[1]

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- *Premise of the study:* Large genera provide remarkable opportunities to investigate patterns of morphological evolution and historical biogeography in plants. A molecular phylogeny of the species-rich and morphologically and ecologically diverse genus *Mimosa* was generated to evaluate its infrageneric classification, reconstruct the evolution of a set of morphological characters, and establish the relationships of Old World species to the rest of the genus.
- *Methods:* We used *trnD-trnT* plastid sequences for 259 species of *Mimosa* (ca. 50% of the total) to reconstruct the phylogeny of the genus. Six morphological characters (petiolar nectary, inflorescence type, number of stamens, number of petals, pollen type, and seismonasty) were optimized onto the molecular tree.
- *Key results: Mimosa* was recovered as a monophyletic clade nested within the *Piptadenia* group and includes the former members of *Schrankia*, corroborating transfer of that genus to *Mimosa*. Although we found good support for several infrageneric groups, only one section (*Mimadenia*) was recovered as monophyletic. All but one of the morphological characters analyzed showed high levels of homoplasy. High levels of geographic structure were found, with species from the same area tending to group together in the phylogeny. Old World species of *Mimosa* form a monophyletic clade deeply nested within New World groups, indicating recent (6–10 Ma) long-distance dispersal.
- *Conclusions:* Although based on a single plastid region, our results establish a preliminary phylogenetic framework for *Mimosa* that can be used to infer patterns of morphological evolution and relationships and which provides pointers toward a revised infrageneric classification.

Key words: biogeography; character evolution; dating analysis; Mimosoideae; molecular phylogeny; *trnD-trnT*; infrageneric classification.

"The foliage of M. viva is said to form extensive mats in low-lying pasture and, being instantly sensitive to shock, provides a canvas for ephemeral graffiti drawn upon it with a stick or finger." (Barneby, 1991)

The phenomenon of large genera and the fact that most large angiosperm genera remain poorly known, especially in terms of their patterns of morphological and geographic diversification, represents a formidable challenge for botanists (Frodin, 2004; Rønsted et al., 2007). The fact that most infrageneric classifications have been based on small numbers of conspicuous morphological characters that often turn out to be homoplastic, and the frequent lack of sufficient morphological diagnosability that coincides with robustly supported monophyletic clades have meant that large and complex groups have been considered to be "unclassifiable" (e.g., Carine and Scotland, 2002). However, these issues remain relatively unexplored for the majority of species-rich genera. Large and geographically widespread genera can also reveal much more comprehensively than has been possible to date the extent to which phylogenies are geographically structured and whether or how that relates to ecological preferences (Schrire et al., 2009). Finally, such genera, if they are distributed across more than one continent, also provide opportunities for testing the hypothesis that many transcontinental disjunctions can be attributed to long-distance dispersal rather than vicariance (Renner, 2004).

Mimosa L. is one of the largest genera in the legume family with more than 500 species distributed mainly in the neotropics with ca. 40 species occurring in the Old World. *Mimosa* species grow in a diverse array of habitats including lowland tropical rainforest, savanna, tropical and subtropical dry forest and thorn scrub, mid-elevation subtropical forest, desert, grassland, and

[1]Manuscript received 21 December 2010; revision accepted 13 April 2011.

The authors thank the following people and institutions that helped with field collections or provision of plant material: E. James, the Millenium Seed Bank Project-Kew Gardens, S. de Faria, M. T. Schifino-Wittmann, N. Dahmer, R. Eastwood, J. Sutherland, G. Elliot, F. Reis, B. Boddey, E. Gross, G. Lewis (K), G. Salazar (MEXU), C. Proença (UB), S. Harris (FHO), A. Martínez, S. Camargo (UAMIZ), M. Sousa, J. Nascimento, T. Pennington, M. Luckow, J. Wood, F. Inches (RBGE), M. Atahuachi, and C. Fagg, and the authorities of Brazil and Mexico for permission to collect plant material (IBAMA authorization n. 02001.007621/2005), and also all managers for permission to collect in their properties. D. Spence and N. Caithness, Oxford Univ. E-Science Centre for help running BEAST on the National Computing Grid, the Clarendon Fund, Wolfson College, and the Systematics Association for support to M.F.S. during his stay at the University of Oxford, and the Royal Society for support to C.E.H.

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doi:10.3732/ajb.1000520

wetland. The genus is particularly diverse in open vegetation and is rich in narrowly restricted endemics. Major concentrations of species diversity and endemism are located in Central Brazil, subtropical South America (Paraguay, Argentina, Uruguay, and southern Brazil), and Mexico, with secondary clusters of species diversity in the Andes, the Caribbean, and Madagascar (Barneby, 1991; Grether et al., 1996; Simon and Proença, 2000; Villiers, 2002). More than a quarter of the species of *Mimosa* are restricted to the Cerrado, the savanna biome of central South America where highland endemics are abundant (Simon and Proença, 2000). Mexico, with more than 100 species, is also remarkable for its high levels of *Mimosa* endemism (Grether et al., 1996). During the preparation of this study, a draft world checklist of *Mimosa* was assembled (M. Simon, R. Grether, and C. Hughes, unpublished manuscript), including ca. 536 described species. Most of them are distributed in the Americas (496) from the United States to Argentina, 34 occur in Madagascar (32 endemics), and only a few in east Africa and south Asia (Appendix S1, see Supplemental Data with the online version of this article). Although it is clear that most of the globally widespread species of *Mimosa* are recently introduced neotropical invasives, it is possible that a few species have native pantropical distributions (Barneby, 1991).

Some mimosas have the reputation for being among the world's most notorious invasive weeds, throughout much of tropical Africa, Asia, and Oceania. One species, *M. pigra*, is among the 100 most invasive organisms on the planet (Lowe et al., 2000). In contrast to this handful of widespread pantropical weeds, the majority of species are globally rare, with numerous narrowly restricted endemics (e.g., Simon and Hay, 2003; Särkinen et al., 2011). Mimosas thus span the complete spectrum of modern geographic range sizes. Many species of *Mimosa* are economically and socially important, being used in reforestation (*M. caesalpiniifolia*), timber production (*M. scabrella*), as medicinal plants (*M. tenuiflora*), and as a source of firewood by subsistence farmers (Rachie, 1979; Camargo-Ricalde et al., 2001). Their ability to fix nitrogen (Reis et al., 2010) and grow quickly make them important plants for soil conservation and enrichment, and some species have been used in agroforestry systems and ecological restoration (Franco and Faria, 1997; Dhillion and Camargo-Ricalde, 2005). Flowers of several *Mimosa* species are also a major source of nectar for honey production (Villanueva, 1994; Fagundez and Caccavari, 2006; Sodre et al., 2007). *Mimosa* is also well known for its seismonastic leaves, prompting specific epithets such as "sensitiva", "pudica" (sold as an entertaining "pet plant"), "casta" and "viva" for species having some of the most striking examples of rapid movement of leaves and leaf parts in response to touch. Thus far, the chemical and molecular bases for leaf movements have been investigated (Allen, 1969; Ueda and Nakamura, 2007), but little is known about how many times this trait evolved in *Mimosa*.

In his seminal taxonomic account of the legume subfamily Mimosoideae, Bentham (1875) divided *Mimosa* into sections *Habbasia* (diplostemonous species) and *Eumimosa* (haplostemonous species) and proposed a number of minor groups. An authoritative taxonomic monograph for the New World species built on Bentham's system and extensively increased both the infrageneric groups and the number of species (Barneby, 1991). The main changes proposed by Barneby (1991) to Bentham's (1875) system were recognition of section *Mimadenia*, based on the presence of leaf nectaries, the division of section *Habbasia* (sensu Bentham) into two sections (*Habbasia* and *Batocaulon*), the inclusion of the genus *Schrankia* Willd. within *Mimosa* as series *Quadrivalves*, plus a major reordering into series and subseries of the haplostemonous mimosas of Bentham's section *Eumimosa* (= sections *Mimosa* and *Calothamnos* of Barneby). Because Old World species were not included in Barneby's (1991) monograph, the placement of these species within the classificatory structure of the American species remain to be determined. A taxonomic account of the Malagasy species did not attempt to relate them to Barneby's classification (Villiers, 2002). Despite the marked increment produced by Barneby's (1991) revision, where 130 new species and around 200 new infraspecific taxa were added to the genus, the pace at which new *Mimosa* taxa continue to be described is remarkable. Around 40 new taxa (35 new species) have been described and a few nomenclatural updates published since Barneby's revision (Villiers, 1990, 2002; Villareal, 1992; Barneby, 1993, 1997; Turner, 1994a–c; Grether and Martínez-Bernal, 1996; Glazier and Mackinder, 1997; Fortunato and Palese, 1999; Queiroz and Lewis, 1999; Grether, 2000; Silva and Secco, 2000; Izaguirre and Beyhaut, 2002, 2003; Atahuachi and Hughes, 2006; Lefevre and Labat, 2006, Lewis et al., 2010; Simon et al., 2010; Morales and Fortunato, 2010; Särkinen et al., 2011).

Alongside his infrageneric classification, Barneby (1991) proposed a series of hypotheses for the evolution of a number of prominent morphological and anatomical characters including habit, armature, indumentum, foliage, pollen, and reproductive structures (Table 1). Barneby's set of evolutionary sequences for *Mimosa*, in which primitive and derived character states were proposed is explicit, but these have never been subject to a comprehensive cladistic analysis. A few previous higher level phylogenetic studies of mimosoid legumes using DNA sequences have included small numbers of species of *Mimosa* (Luckow et al., 2003, 2005). An analysis focused on the genus *Piptadenia* s.l. (Jobson and Luckow, 2007) included nine species of *Mimosa* and provided strong support for the monophyly of the genus and its placement within the *Piptadenia* group, as previously proposed (Lewis and Elias, 1981) and envisaged by Barneby (1991). A preliminary species-level molecular phylogeny sampled 28 mainly southern South American species (Bessega et al., 2008), but the very sparse taxon sampling limits its utility to assess Barneby's classification and hypotheses of character evolution. Here we present a densely sampled molecular phylogeny of *Mimosa*, including representatives of almost all the major infrageneric groups and about half of the described species. The evolution of selected morphological characters, including several key characters that are prominent in defining the sectional classification, plus the variation in seismonasty, are investigated. The main goals of this study were to (1) test the monophyly of the groups proposed in Barneby's infrageneric classification, (2) analyze the relationships of the Old World species to the rest of the genus, (3) provide a comparative framework to investigate the evolution of key morphological characters previously used to differentiate major infrageneric groups and test the evolutionary sequences proposed by Barneby (1991), and (4) provide a time frame for the diversification of major clades.

MATERIALS AND METHODS

Taxon sampling—The analysis presented here includes 284 accessions of *Mimosa*, representing taxa from all five sections and 37 of the 41 series proposed by Barneby (1991), plus half of the Old World species and 13

outgroups. Three of the four series not represented here (*Ephedroideae*, *Rondonianae*, and *Pseudocymosae*) are monospecific, while series *Piresianae* has just five species and could not be sampled due to lack of material. The 259 species sampled were chosen to cover the native geographic and ecological range of the genus (Appendix S1). Most samples were collected in the field (silica-dried leaves), but herbarium specimens and seedlings grown from seed collections in the greenhouse were also used. For a few widely distributed species, multiple accessions were included, either representing specimens from distant locations across the range or different infraspecific taxa. Accessions with taxon names, voucher specimens, locations, and GenBank accession numbers are listed in Appendix 1. Most sequences used here come from previously published studies (Simon et al., 2009; Särkinen et al., 2011), while 17 new sequences are published for the first time (GenBank accessions JF694255–JF694271). Nomenclature follows Barneby (1991), Villiers (2002) for the Malagasy species, Gamble (1920) for the Asian species, Brenan and Brummitt (1970) for the African species, with relevant post-Barneby updates (Brummitt, 1993; Turner, 1994a–c; Glazier and Mackinder, 1997; Grether, 2000) and additions (as noted earlier).

DNA extraction, amplification, and sequencing—Total DNA from silica-dried leaves or herbarium material was isolated using the DNeasy plant mini kit (Qiagen, Crawley, UK). After initial screening of a set of 16 plastid DNA sequence loci (Appendix S2, see online Supplemental Data), the *trnD-trnT* intergenic spacer was selected as the most variable and informative plastid locus for *Mimosa*. This region comprises the fragment located between a primer pair anchored within the $trnD^{guc}$ and $trnT^{ggu}$ genes including a noncoding intergenic spacer (ca. 85%) and the embedded $trnY^{GUA}$ and $trnE^{UUC}$ genes, and also two regions of mononucleotide repeats (poly A/T). For most taxa, the whole region was amplified in a single PCR reaction using primers trnD2 (designed for this study) and $trnT^{ggu}$ (Shaw et al., 2005). For degraded DNA templates derived from herbarium material, amplifications were performed using internal primers $trnE^{uuc}$ and $trnY^{gua}$ (Shaw et al., 2005) in combination with the external primers, and in some cases another newly designed primer, trnT2. The primers used in this study, in 5′ to 3′ orientation, are as follows: trnD2 (GTG TAC AGC ATG CAT ATT CTT ACG), $trnY^{gua}$ (CCG AGC TGG ATT TGA ACC A), $trnE^{uuc}$ (AGG ACA TCT CTC TTT CAA GGA G), $trnT^{ggu}$ (CTA CCA CTG AGT TAA AAG GG), and trnT2 (GAC GTA TCG CCG AGT AAT TCC).

Polymerase chain reactions (PCR) were conducted in a total volume of 25 μL, containing ~5–20 ng of DNA template, 1× Buffer, 0.5 mol/L of betaine, 1.5 mmol/L of $MgCl_2$, 0.1 mmol/L of each dNTP, 0.5 μmol/L of each primer and 0.6 U of *Taq* polymerase (Yorkshire Bioscience, UK). PCR conditions were 94°C for 5 min; 30 cycles of 45 s at 94°C, 1 min at 55°C and 1 min at 72°C; followed by a final extension of 5 min at 72°C. PCR products were cleaned using exonuclease I and shrimp alkaline phosphatase (Exo/SAP) and sequenced in four reactions using the two PCR primers and the two internal primers, following Big Dye v. 3.1 chemistry (Applied Biosystems, Warrington, UK). Problems in sequencing caused by poly A/T regions were overcome by performing four sequencing reactions. Consensus sequences from the four sequence strands were assembled using Sequencher (v. 3.1; GeneCodes Corp., Ann Arbor, Michigan, USA), and then imported into BioEdit (Hall, 1999) for alignment using the program Clustal W (Thompson et al., 1994; spawned by BioEdit using default parameters) and manual edition. Regions of problematic alignment, where homology could not be determined with confidence, were considered unalignable and excluded from the data set. Unambiguous indels were coded using the program SeqState (Müller, 2005), following the simple gap coding method of Simmons and Ochoterena (2000) and were used in the parsimony analysis. Indels associated with mononucleotide repeats, common features in our data set, were not coded as gaps since these regions are particularly prone to length mutations. A full data set including coded indels is available in the database TreeBase (http://treebase.org, study accession number S11700).

Phylogenetic analyses—Parsimony analysis was conduced using the program Nona (Goloboff, 1993), spawned from Winclada (Nixon, 2001). Tree searches employed 5000 replicates, holding 50 trees in each search, using the tree bisection and reconnection (TBR) strategy and branch swapping, holding a maximum of 100 000 most parsimonious trees. Additional searches for possible shorter trees were conducted using the parsimony ratchet (Nixon, 1999), with four independent runs of 200 iterations each, holding five trees per replicate and randomly reweighting 100 characters and constraining 10% of the nodes in each iteration. Strict consensus bootstrap percentages were computed with 1000 replicates and 10 tree-bisection reconnections, holding 10 trees per replicate.

A Bayesian analysis for phylogenetic reconstruction and to estimate divergence times was conducted under the uncorrelated lognormal relaxed molecular clock approach implemented in the program BEAST version 1.4.8 (Drummond and Rambaut, 2007). The GTR + G + I nucleotide substitution model was chosen based on the Akaike information criterion as implemented in the program Modeltest (Posada and Crandall, 1998). Divergence time estimates for *Mimosa* were based on an initial higher level family-wide analysis of a large *matK* data set containing 839 terminals (Simon et al., 2009). Age estimates (mean and 95% credibility intervals) for the *Mimosa* crown node (24.0 Ma, CI [18.0, 30.6]) and the section *Mimadenia* (clade A) crown node (16.6 Ma, CI [10.1, 23.6]) obtained from the family-level analysis were used as calibration constraints using a normal distribution prior. Three runs of 10^7 generations each were performed, sampling every 10^4 generations. Results were assessed to have reached stationarity and convergence using the program Tracer version 1.4 (Rambaut and Drummond, 2007), and data from multiple runs were combined after exclusion of burn-in trees. All estimated parameters had sufficient effective sample sizes (ESS), in most cases well above the minimum of 200 recommended in the BEAST manual.

Evolution of morphological characters—We selected a subset of five conspicuous characters (Table 1) that play a central role in Barneby's classification, to investigate the evolution of these characters as putative synapomorphies that might provide diagnosability for well-supported infrageneric groups within *Mimosa*. In addition, we investigated the evolution of rapid seismonastic leaf movement in the genus, which was treated here as a morphological character.

Petiolar nectaries—Extrafloral nectaries are a common feature of many genera of Mimosoideae and Caesalpinioideae, and are often related to mutualistic relationships between plants and ants, where the plant provides food to ants, and in return, receives protection against herbivores and/or seed predators (McKey, 1989). The presence of petiolar nectaries was a key character used by Barneby to distinguish section *Mimadenia*, which in his interpretation retained this ancestral condition shared with closely related Piptadenioid sister groups (Table 1).

Type of inflorescence—The reduced flowers of *Mimosa* are grouped into compact inflorescences that can be either a capitulum or a spike. Although intermediates (ellipsoidal capitula) are found in some species, in most cases, the inflorescences are clearly either globose or spicate, and the type of inflorescence has been an important character to define groups in *Mimosa* (e.g., series *Dystachyae* and *Leiocarpae*). Barneby (1991) argued that the spike is the plesiomorphic condition in *Mimosa* (Table 1), but recognized many reversals from capitulum to spike.

Number of stamens—The number of flower parts, and especially the number of stamens, has dictated the tribal classification of the mimosoids and was also central in the infrageneric classification of *Mimosa* (Bentham, 1875; Lewis and Elias, 1981; Barneby, 1991). Haplostemonous flowers in *Mimosa* are thought to

TABLE 1. Summary of evolutionary progressions for morphological traits in *Mimosa* as hypothesized by Barneby (1991).

Character	Anterior / Primitive	Posterior / Derived
Petiolar nectary	Present, functional	Reduced to nonfunctional spicule, obsolete
Inflorescence	Axillary; flowers spicate, all hermaphroditic	Paniculate, pseudoracemose, radical; flowers capitate, the lower staminate
Corolla	5-(6)-merous; the lobes membranous, 1-nerved	4-, then 3-merous; lobes either thickened or several-nerved
Androecium	Diplostemonous, filaments free, connective ovate	Haplostemonous, filaments monadelphous, connective orbicular
Pollen	In large or moderate, compound tetrads	In small, simple tetrads

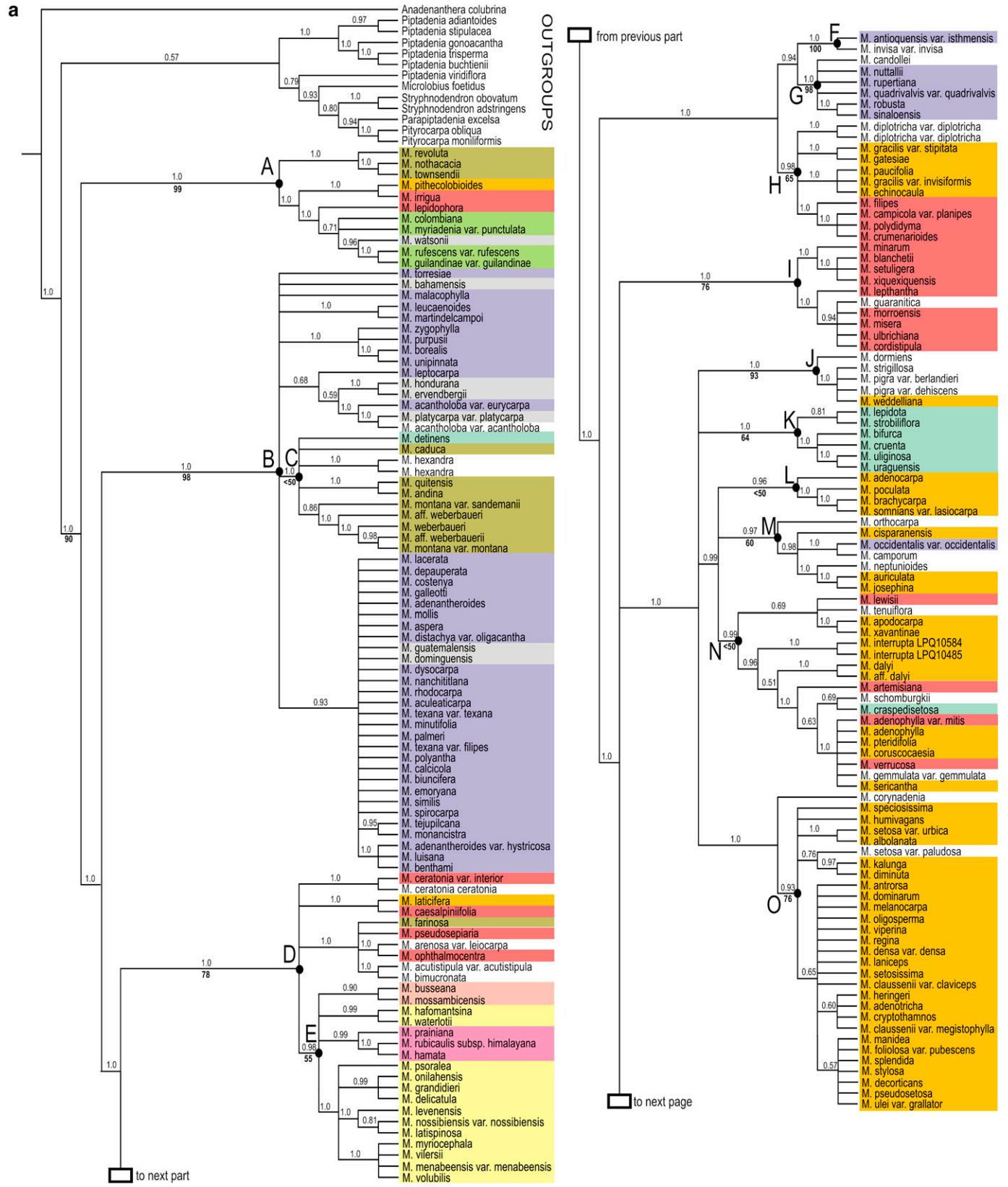

Fig. 1. Phylogeny of *Mimosa* based on DNA sequences of the *trnD-trnT* noncoding plastid locus. The 50% majority-rule consensus tree from a Bayesian analysis. Letters on nodes define well-supported clades discussed in the text, and colors represent geographic distribution. Numbers above and below nodes are posterior probabilities and bootstrap percentages from the parsimony analysis (shown only for major clades), respectively. The asterisk represents the only lettered clade not present in the parsimony strict consensus tree.

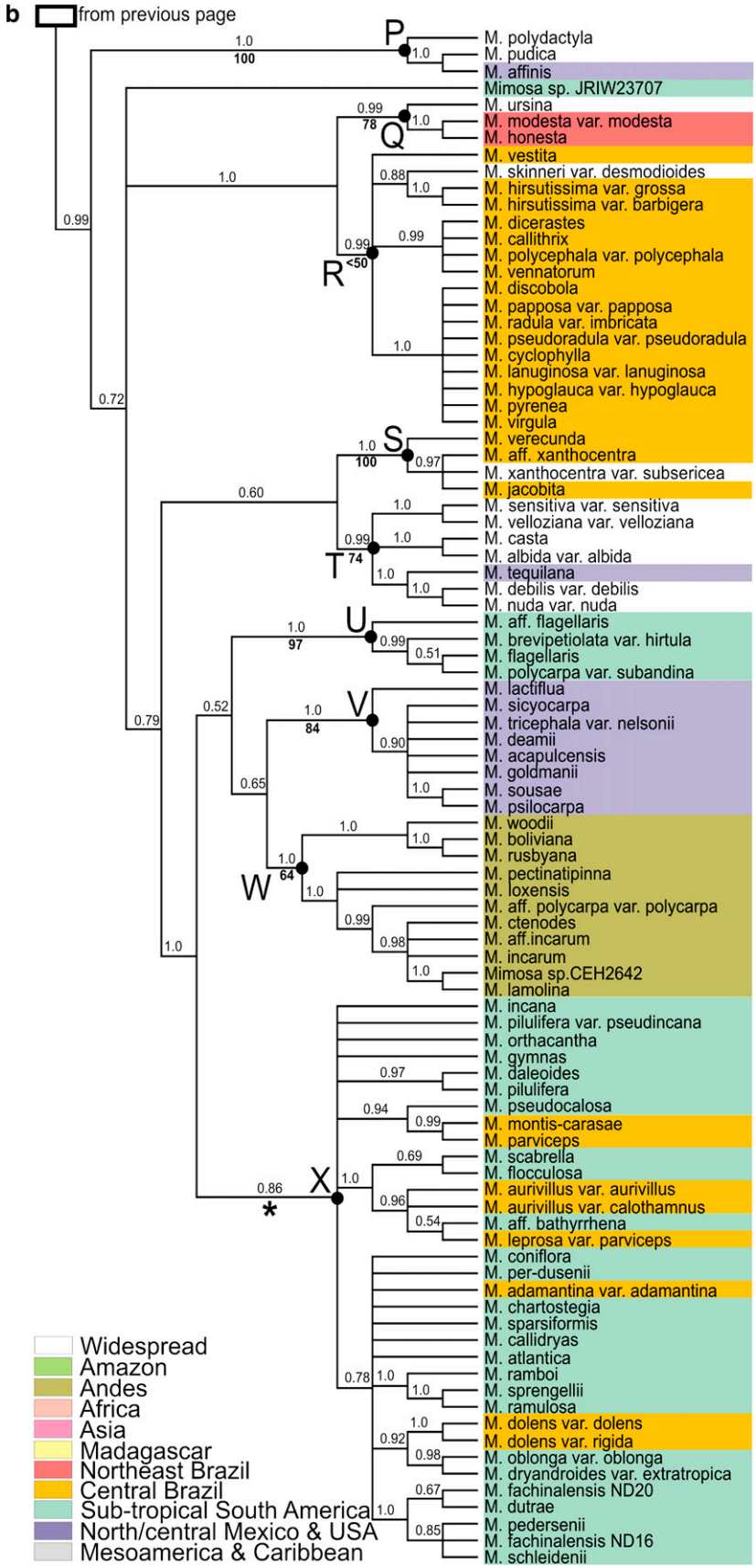

Fig. 1. Continued

have evolved via suppression of the antepetalous whorl of a putative primitive diplostemonous androecium, which is predominant in the *Piptadenia* group, and are thus considered to be the derived state (Barneby, 1991; Table 1).

Number of petals—The corolla in *Mimosa* can have three, four, five, or more rarely six petals, although some random variation within species has been recorded (Barneby, 1991). Based on outgroup comparison with other members of the *Piptadenia* group which all have five petals, Barneby (1991) suggested that pentamerous flowers are plesiomorphic, with tetramerous and trimerous flowers representing pogressive apomorphic specializations (Table 1).

Pollen type—Pollen in mimosoids is frequently arranged in polyads. In *Mimosa*, polyads of four (tetrads), eight (bi-tetrads), 12, or 16 grains, have been extensively characterized (Guinet, 1969; Caccavari, 1986, 1988, 1989, 2002; Lima et al., 2008). Caccavari (1988, 1989) hypothesized that pollen in *Mimosa* evolved from simple small tetrads to large and more complex polyads, contrasting with Barneby's (1991) idea in which pollen in tetrads occurs in the morphologically most derived and specialized groups in the genus (Table 1).

Leaf movement—The sensitivity of *Mimosa* leaves to touch (seismonasty) varies widely across the genus. Some species close their leaflets almost instantly when touched, while others respond very slowly or are insensitive to any stimulus. Despite the continuum in the degree of seismonasty across the genus, we have chosen to recognize only two character states: absence of seismonasty including very slow leaf movements and rapid seismonastic leaf movements, in which the leaflets can close in less than five seconds.

The morphological data set (online Appendix S3) is based primarily on published studies (Gamble, 1920; Brenan and Brummitt, 1970; Barneby, 1991, 1993; Grether and Martínez-Bernal, 1996; Fortunato and Palese, 1999; Grether, 2000; Villiers, 2002; Atahuachi and Hughes, 2006). Data on pollen type were also compiled from the literature (Guinet, 1969; Caccavari, 1986, 1988, 1989, 2002; Grether and Martínez-Bernal, 1996; Flores-Cruz et al., 2006; Martínez-Bernal, 2003; Lima et al., 2008; Buril et al., 2010) plus new data (R. Grether, unpublished data) and were available for 170 of the 297 terminals. Information on seismonastic leaf movements has been gathered mostly from our own field experience and tests in the greenhouse with more than 30 species, because there are no systematic published data on this beyond a few records of leaf movements reported by Barneby (1991). Although our knowledge about the extent of seismonasty remains limited, the available data provide some preliminary evidence about how many times seismonasty has evolved in *Mimosa* and how this trait is distributed among groups.

Ancestral character state reconstruction analysis was used to investigate the evolution of these six characters in *Mimosa*, using trees derived from the *trnD-trnT* Bayesian analysis as a phylogenetic framework. All traits were coded as discrete bistate or unordered multistate characters and optimized onto the 50% majority-rule consensus trees under a maximum parsimony criterion using the package Mesquite version 2.01 (Maddison and Maddison, 2007). To account for topological uncertainty, the procedure "Trace over trees" was used to summarize ancestral state reconstructions over a set of 1000 Bayesian trees sampled at stationarity. This approach was used to identify unequivocal changes in character states across the tree and thus shed light on the morphological evolution of *Mimosa*. In cases where there is variation within a species, for example, in a species where flowers can have either four or five petals, the species was coded as polymorphic.

RESULTS AND DISCUSSION

trnD-trnT data set—The aligned *trnD-trnT* matrix comprises 2262 bp after exclusion of regions of ambiguous alignment. A total of 395 (17.5%) substitutions were parsimony-informative, with 361 of these (16.0%) informative within *Mimosa*. Intergenic spacers are susceptible to different types of structural mutations such as insertions, deletions, and inversions (Kelchner, 2000). Extreme examples in our data set are a 225-bp autapomorphic inversion in *M. detinens* (excluded from the analysis) and a 300-bp deletion in *M. dysocarpa*. Unambiguous gaps, many of them larger than 10 bp, were common across the whole alignment, and a total of 102 informative indels were coded and used in the parsimony analysis, making up 21% of all informative characters. Unalignable regions comprising 137 sites were excluded.

The levels of informative *trnD-trnT* variation in *Mimosa* are high compared to other noncoding plastid regions, in line with findings that the *trnD-trnT* spacer is one of the most variable plastid regions (Shaw et al., 2007) and thus useful for phylogenetic analyses at the species level. Furthermore, in *Mimosa*, the *trnD-trnT* locus is ca. 500 bp longer than the average of ca. 1000 bp reported by Shaw et al. (2005) and therefore provides a larger number of variable sites. In fact, the *trnD-trnT* locus represents a promising option to resolve relationships across the mimosoid subfamily as a whole, given that present mimosoid phylogenies suffer from lack of resolution and low substitution rates compared to other legume groups (Luckow et al., 2003, 2005; Lavin et al., 2005).

Phylogenetic analysis and major Mimosa clades—The parsimony analysis discovered the maximum set of 100 000 equally parsimonious trees of 1123 steps (CI = 0.56, RI = 0.92). A parsimony ratchet found an additional 971 trees of the same length, which were combined to produce a strict consensus tree (online Appendix S4). The Bayesian analysis produced a very similar topology to the parsimony analysis, although somewhat better resolved (Fig. 1). All the major clades are present in both analyses, except clade X, which is absent in the parsimony tree, but this does not represent conflicting topology. Most nodes are more strongly supported in the Bayesian tree than in the parsimony tree, even considering that bootstrap percentages are more conservative than Bayesian posterior probabilities (Alfaro and Holder, 2006). The majority-rule Bayesian tree (Fig. 1) serves as the basis for most of the subsequent analyses and discussions in this paper.

Mimosa was recovered as monophyletic with robust support in both parsimony and Bayesian analyses and includes the former members of the genus *Schrankia* (clade G), which are deeply nested within *Mimosa* in the molecular analysis, corroborating their transfer to *Mimosa* by Barneby (1991). In addition, there is also strong support for the inclusion of the monospecific genus *Schrankiastrum* Hassler within *Mimosa* (Barneby, 1984). Although we have not sampled *S. insigne* Hassler [=*M. insignis* (Hassler) Barneby], the position of *M. dalyi*, its putative sister species based on morphological evidence, deeply nested within clade N (Fig. 1), corroborates Barneby's (1984) interpretation.

The precise sister group relationships between *Mimosa* and other genera of the *Piptadenia* group are still not clear, especially in the Bayesian tree. The parsimony strict consensus tree (Appendix S4) suggests that the Eupiptadenia clade (*Piptadenia* sensu Jobson and Luckow, 2007) could be the sister group of *Mimosa*, although receiving no bootstrap support. In a study focused on the polyphyletic genus *Piptadenia* based on *matK* and *trnL-trnF* sequences, Jobson and Luckow (2007) also found indications for the Eupiptadenia clade as sister to *Mimosa*, although again with low support. This relationship received moderate (80%) bootstrap support in a parsimony analysis of three concatenated loci (*matK*, *trnL-trnF*, and *trnD-trnT*) for a small subset of 12 *Piptadenia* group taxa (M. Simon et al., unpublished data). Overall, these results agree with the hypothesis of a close relationship between *Piptadenia* s.l. and *Mimosa* based on morphology (Barneby, 1991; Lewis and Elias, 1981) and also with a higher level legume phylogeny (Simon et al., 2009).

When we come to examine the new *Mimosa* phylogeny in relation to Barneby's (1991) infrageneric classification, only

sections *Mimadenia* and *Calothamnos* (only recovered in the parsimony analysis) are monophyletic (Table 2). Section *Mimadenia*, which shares the plesiomorphy of extrafloral nectaries with the outgroup genera, is robustly supported as sister to the rest of *Mimosa* in the *trnD-trnT* analysis (Fig. 1), in line with Barneby's classification and hypothesized evolutionary sequence. Sections *Batocaulon* and *Habbasia* form an extensive paraphyletic grade with members of the two sections intermingled (Fig. 2a). Section *Calothamnos* is nested within section *Mimosa* and is only well-supported in the parsimony analysis due to a shared synapomorphic indel. There is no support for the idea that section *Calothamnos* is derived from within section *Batocaulon*, as hypothesized by Barneby (1991), who segregated it from the other haplostemonous species. Indeed, section *Mimosa* would be rendered monophyletic if *Calothamnos* is incorporated within it, which would correspond, with just a few exceptions (see Fig. 2d), to the group of haplostemonous mimosas envisaged by Bentham (1875) in his section *Eumimosa*. Similar results, based on a smaller taxon sample, were found by Bessega et al. (2008).

TABLE 2. Infrageneric classification of *Mimosa* (Barneby, 1991) with the corresponding clades in the molecular phylogeny presented here (Fig. 1) and the status of sections and series. The monophyly of some groups could not be assessed because of lack of resolution in the tree or undersampling. * Series not sampled in this study.

Section / Series	Corresponding clade	Monophyletic
***Mimadenia* Barneby**	A	yes
Myriadeniae Barneby	A	monotypic
Glanduliferae Benth.	A	no
Revolutae Barneby	A	monotypic
Nothacaciae Barneby	A	yes
***Batocaulon* DC.**	B,C,D,E,F,G,H,I,K,M,N	no
Distachyae Barneby	B	no
Andinae Barneby	B(C)	unresolved
Acanthocarpae Benth.	B	unresolved
Acantholobae Barneby	B	yes
Boreales Barneby	B	no
Leiocarpae Benth.	B,D,N	no
Bimucronatae Barneby	B(C),D,N	no
Leucaenoideae Barneby	B	unresolved
Rubicaules Benth.	B,D(E),G	no
Fagaracanthae Barneby	B	undersampled
Bahamenses Barneby	B	monotypic
Farinosae Barneby	B(C),D	no
Ephedroideae Benth.*	—	—
Echinocaulae Barneby	H	monotypic
Paucifoliatae Benth.	H	no
Glandulosae (Benth.) Barneby	L	no
Stipellares Benth.	K	yes
Auriculatae Barneby	M	monotypic
Caesalpiniifoliae Benth.	D	yes
Ceratoniae Barneby	D	undersampled
Cordistipulae Barneby	I	yes
Campicolae Barneby	H	undersampled
Filipedes Barneby	H	no
Quadrivalves Barneby	G	no
Plurijugae Karsten	B,F	no
***Calothamnos* Barneby**	X	unresolved
***Habbasia* DC.**	J,L,M,O	no
Setosae Barneby	O	no
Pachycarpae Benth.	O	no
Habbasia DC.	J	yes
Bipinnatae DC.	L	yes
Neptunioideae Barneby	M	no
Rondonianae Barneby*	—	—
Rojasianae Barneby	M	undersampled
Pseudocymosae Hassler*	—	—
Piresianae Barneby*	—	—
Mimosa L.	P to X	no
Myriophyllae Benth.	X	unresolved
Mimosa L.	P,R,S,T,U,V,W,X	no
Modestae Benth.	Q,R	no

Despite these notable disagreements at sectional level between the results presented here and Barneby's (1991) classification, many of Barneby's series and subseries within sections were recovered as monophyletic (Table 2). Insufficient taxon sampling or lack of resolution in some parts of the phylogeny prevents the evaluation of all infrageneric groups, most notably within series *Mimosa*, which was divided by Barneby into 37 subseries. Because of undersampling, these groups are not discussed further here. We focus our discussion on the 24 well-supported clades A–X (Fig. 1) and review these groups in relation to Barneby's (1991) infrageneric classification (Appendix 2).

Neither taxon nor character sampling in this study were designed to test species boundaries or within-species relationships. However, there are indications that some species for which multiple accessions were included do not form monophyletic clades. These include *M. weberbaueri*, *M. montana* (clade C) (see Särkinen et al., 2011), *M. gracilis* (clade H), *M. setosa, M. claussenii* (clade O), *M. polycarpa* (clades U and W), and *M. fachinalensis* (clade X). More detailed studies with rangewide sampling of multiple accessions and preferably including a nuclear locus will be required to investigate the status of these species and their infraspecific variants.

Evolution of morphological characters—Optimization of a set of morphological characters onto the *trnD-trnT* phylogeny allowed the reconstruction of character states across the tree, sheding light on the morphological evolution of *Mimosa* (Figs. 2, 3). Character optimizations were unequivocal for most nodes in the Bayesian trees. The character optimizations across the 1000 different Bayesian trees sampled at stationarity produced, in almost all cases, the same result as the findings presented in the majority-rule consensus tree. Levels of homoplasy, as measured by the consistency index (CI) and the retention index (RI), varied widely between characters (Table 3), varing from no homoplasy (petiolar nectary) to highly homoplastic (inflorescence type).

Petiolar nectaries—For *Mimosa*, the presence of extrafloral nectaries is plesiomorphic and restricted to species of section *Mimadenia* (clade A), in line with Barneby's (1991) hypothesis. Within *Mimosa*, the petiolar nectary provides a conspicuous diagnostic character for that section. The ancestral character reconstruction suggests that section *Mimadenia* retained this ancestral character state, which is present in all species of the *Piptadenia* group (outgroups), but absent from the rest of the genus *Mimosa* (Fig. 2b). This finding was consistent across all of the sampled Bayesian trees. There is no indication of reacquisition of petiolar nectaries (reversal) in any other lineages within *Mimosa*, indicating lack of homoplasy in this character and its suitability as a diagnostic character (Table 3).

Marazzi et al. (2006) hypothesized that the presence of extrafloral nectaries in *Senna* (Caesalpinioideae) could represent a key innovation in terms of plant defense strategies that promoted large-scale diversification and colonization of a wide range of habitats and climates on different continents. They

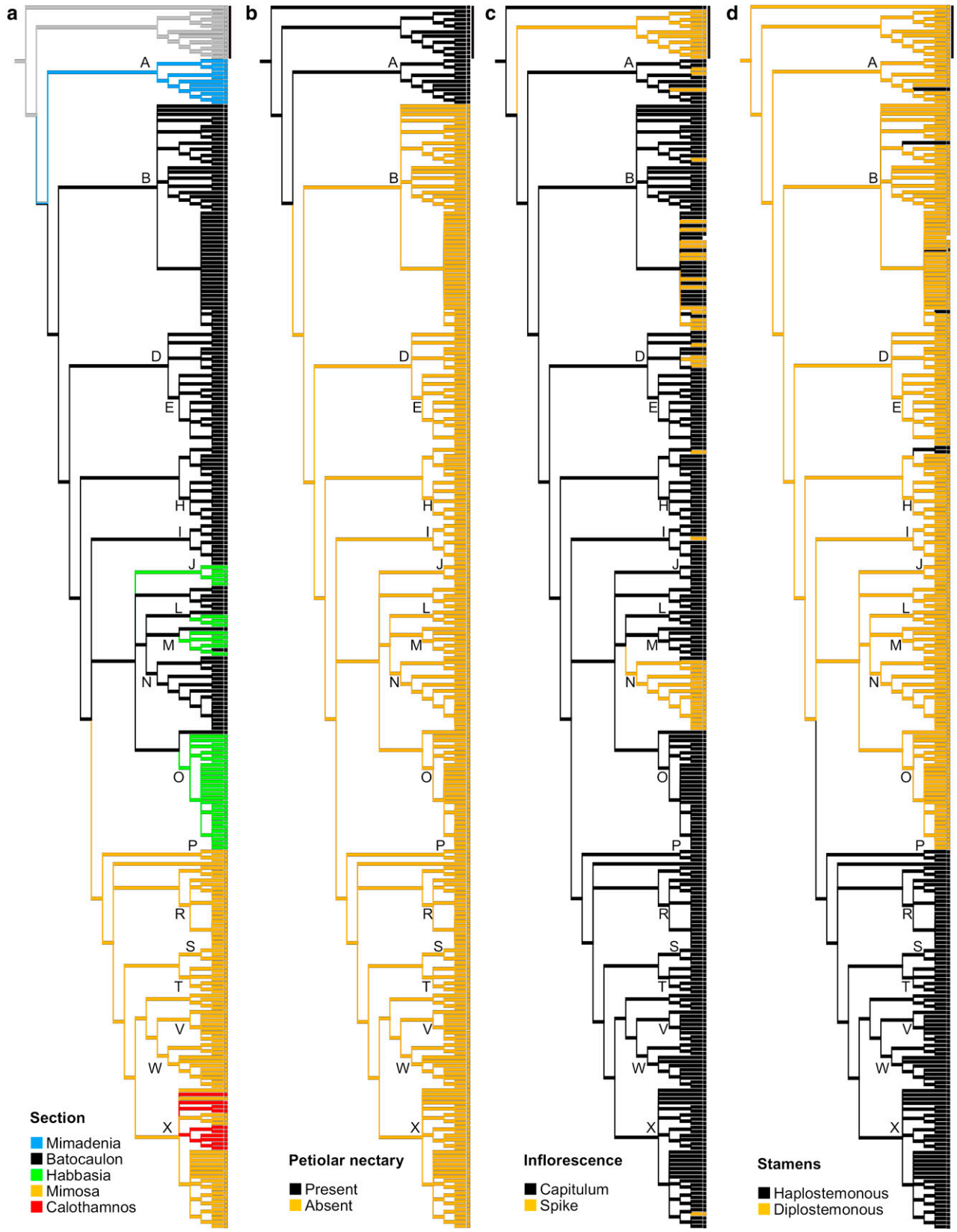

Fig. 2. Infrageneric classification and morphological evolution in *Mimosa*. (a) Mapping of Barneby's (1991) five sections onto the *trnD-trnT* gene tree, showing that most infrageneric sections are not monophyletic. (b–d) Character optimizations onto a 50% majority-rule Bayesian tree showing the evolution of (b) petiolar nectaries (c) type of inflorescence, and (d) number of stamens.

found that the *Senna* clade characterized by the presence of extrafloral nectaries has a much larger number of species than clades which lack nectaries, and argued that presence of nectary could provide a possible evolutionary innovation that prompted this accelerated diversification (Marazzi and Sanderson, 2010). Conversely, it is notable that in *Mimosa* the derived loss of petiolar nectaries is associated with a much larger clade (515 species) than the group that retained this characteristic (section *Mimadenia*, 15 species). Surveys of other groups are needed to verify whether the presence of extrafloral nectaries and the occurrence of ant mutualisms are related to higher rates of species diversification more widely in plants.

Inflorescence type—Ancestral state reconstruction of this character suggests high levels of homoplasy (Table 3), with frequent shifts between capitula and spikes across the tree (Fig. 2c). Character optimization indicates an unequivocal change from an ancestral spike (the most common state in the outgroup) to a capitulum at the base of the genus *Mimosa*. However, the predominant capitate inflorescences were reversed to spicate several times (Fig. 2c) independently in different lineages: clade A (*M. myriadenia*), clade B (several species), clade D (*M. caesalpiniifolia*, *M arenosa*, *M. ophthalmocentra* and *M. acustistipula*), clade F (*M. invisa*), clade I (*M. xiquexiquensis*), clade N, and clade X. In clade B, spicate species are placed in a large polytomy, shedding no light on the evolution of this character within this group. On the other hand, spikes probably evolved only once in clade N (supported by 523 of the 1000 Bayesian trees), which suggests that the capitulum in *M. lewisii* represents a reversal. In clade X, *M. dutrae* evolved short spikes from a capitulum. It is expected that many more reversals may have occurred in clade X, since many species of section *Mimosa* with spicate inflorescences were not sampled here.

For the most part, Barneby (1991) viewed this as a conservative character only rarely putting species with different types of inflorescences together in the same group. For example, Barneby's placement of the sister species *M. acutistipula* and *M. bimucronata* (Fig. 1), which are virtually identical apart from their inflorescences in spikes and capitula (respectively), in different series, reflects this viewpoint.

Number of stamens—The ancestral diplostemonous condition predominates in *Mimosa*, with switches to haplostemonous flowers hypothesized to have occurred at least six times (Fig. 2d, Table 3), with all these character state transitions unequivocal (i.e., present in all 1000 Bayesian trees). The most relevant transition in terms of classification is the one that segregates a monophyletic group containing the haplostemonous sections *Mimosa* and *Calothamnos* from the rest of the genus. Barneby (1991) hypothesized that Bentham's series *Lepidotae* evolved haplostemony independently of the other haplostemonous mimosas, and on that basis established section *Calothamnos*, segregating it from section *Eumimosa*. However, our results more closely support Bentham's classification where all haplostemonous mimosas were placed in one large group. However, there are a few important exceptions where other haplostemonous lineages are deeply nested within diplostemonous clades: e.g., *M. myriadenia* in clade A, and series *Plurijugae* (clade F), which Bentham (1875) considered to belong within section *Eumimosa*. In contrast, Barneby (1991) correctly interpreted these as independent reductions in stamen number and considered these species unrelated to section *Eumimosa*. In addition, the placements of *M. tejupilcana* and *M. leptocarpa* (clade B) also suggest additional independent switches to haplostemonous flowers.

Number of petals—Number of petals is another highly homoplastic character with multiple unequivocal character state transitions hypothesized by the optimization analysis (Fig. 3a). The ancestral condition in *Mimosa* was unequivocally assigned as five petals, a character state retained from its mimosoid ancestors. This was also the unequivocal ancestral condition in clade A, but not in clade B, where most reconstructions are equivocal, probably because of lack of resolution and due to the frequent switches in petal number. The node subtending the large group made up of clades D–X is assigned as tetramerous by 770 of the Bayesian trees, and this is the predominant state in *Mimosa*. Shifts from tetramerous to trimerous corollas were observed in clade D (*M. ceratonia*, *M. caesalpiniifolia*, and *M. laticifera*), in a subclade nested within clade H (series *Campicolae* and *Filipedes*), and in clade I (series *Cordistipulae*). A reversal from four to five petals (supported by 943 trees) is hypothesized for clade F + G. A few species with six petals occur in clades A (*M. colombiana*) and G, but in both cases these species have a mixture of flowers with five and six petals. Overall, the number of petals is variable within seven of the major clades defined in this study (clades A–D, G, H, and N). Although numerous switches in the number of petals are postulated to have occurred in *Mimosa*, this character still can be a potentially useful diagnostic character for clade I and a few subgroups within major clades. It is important to note that some *Mimosa* species (19 sampled here) have occasional flowers with a different number of petals or sometimes similar proportions of two types of flowers within an inflorescence. An extreme case of variation in floral parts is found in series *Fagaracanthae* where flowers can consistently have from four to five petals (Barneby, 1991).

Pollen type—Polyads comprising eight pollen grains predominate across the outgroups, and this character state is unequivocally optimized as the ancestral state in *Mimosa* (Fig. 3b). An unequivocal change to polyads of 12 grains is hypothesized in a subclade in clade A, although *M. revoluta*, *M. nothacacia*, and *M. townsendii* retained the bi-tetrads. An additional change to a 16-grain polyad is suggested for *M. rufescens* (the only one documented here). Pollen in bi-tetrads characterizes clades B and D, which also unequivocally retained the ancestral state. An unequivocal change from bi-tetrads to tetrads, which is the predominant pollen type in *Mimosa*, is hypothesized to have occurred on the branch leading to the large group comprising clades F–X. Only a single reversal to bi-tetrads is hypothesized to have occurred within this very large group (*M. sinaloensis*, clade G).

Previous attempts to correlate pollen morphology with the infrageneric classification in *Mimosa* have had little success (Caccavari, 1988), largely due to the nonmonophyly of many of the infrageneric groups. Here we show that pollen type is remarkably congruent with the plastid gene tree and that this character presents relatively low levels of homoplasy (Table 3). Our results do not support the hypothesis of pollen evolution in which polyads with higher numbers of grains evolved from tetrads (Caccavari, 1988, 1989), but agree with the evolutionary progressions proposed by Barneby (1991), with large compound polyads as plesiomorphic and tetrads as more derived (Table 1). Other pollen traits not investigated here such as shape and size of the polyads, presence of apertures, and structure of the exine (Caccavari, 1988, 2002), may also be of taxonomic

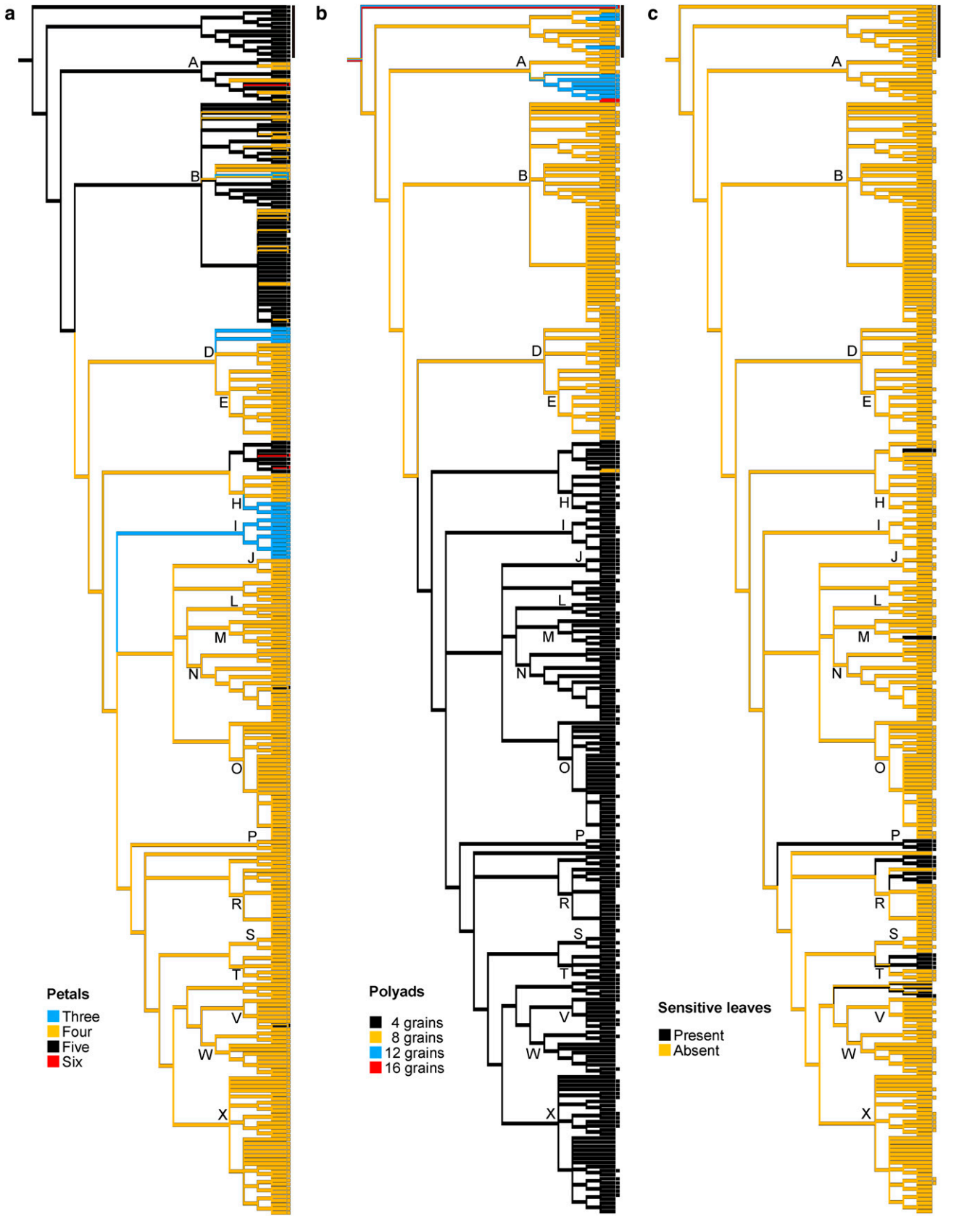

Fig. 3. Morphological evolution in *Mimosa*. Character optimizations onto a 50% majority-rule Bayesian tree showing the evolution of (a) number of petals, (b) pollen type, and (c) sensitive leaves. Missing data are indicated by slightly shorter terminal branches in (b) and (c).

significance and could be explored further. In a comprehensive palynological study of the northeastern Brazilian species of *Mimosa*, Lima et al. (2008) reported the occurrence of monads and dyads in the genus. However, we view their findings with caution. Visual inspection of their images suggests that monads and dyads reported for *M. ursina* (figs. 42–46 in Lima et al., 2008) actually correspond to tetrahedric tetrads, in line with previous data for this species (Grether, 1997). Therefore, species reported as containing monads or dyads by Lima et al. (2008) were instead coded here as having tetrads.

Sensitive leaves—Seismonasty is hypothesized to have arisen independently in eight lineages of *Mimosa* (Fig. 3c), including clades G, M, P, Q, R, T, and U. However, it is important to bear in mind that this trait is present, albeit to a lesser degree, in many other species in the genus. The biological significance of seismonasty is not well known, but probably evolved as a defense mechanism against herbivores or to avoid leaf damage in regions with very wet climates, although this remains to be confirmed experimentally. Detailed studies found different types of nyctinastic (night time) leaf movements within the mimosoid genera *Desmanthus* (Luckow, 1993) and *Leucaena* (Hughes, 1998), in which the pinnae and petiole can move either downward or upward, providing further evidence that patterns of evolution of leaf movements are both complex and evolutionarily labile in mimosoid legumes. The preliminary analysis shown here suggests that rapid leaf movements evolved multiple times in distinct lineages within *Mimosa*, suggesting that the physiological and morphological apparatus required for seismonasty has been recruited recurrently during the evolution of the genus. However, more detailed studies might identify some coherent phylogenetic patterns and also ecological associations related to leaf movement.

Toward a new infrageneric classification of Mimosa—Classifications that reflect evolutionary relationships based on monophyly combined with diagnosability are a widely accepted goal of modern systematics (Carine and Scotland, 2002). Many of the groups of Barneby's (1991) infrageneric classification are shown here to be nonmonophyletic (Table 2). However, several of the 24 strongly supported clades highlighted here lack any obvious diagnostic morphological apomorphies. This is evident from the high degree of homoplasy found in some of the morphological characters investigated, such as number of petals and type of inflorescence (Figs. 2, 3; Table 3). However, it is important to mention that a few clades received strong support from conspicuous morphological characters, such as section *Mimadenia* (clade A; presence of petiolar nectaries) and series *Cordistipulae* (clade I; trimerous flowers).

A more detailed survey of other morphological traits not investigated here (such as armature, indumentum, calyx morphology, and fruit type) may yet reveal reliable characters that define some of these groups and provide the diagnosability sought in modern classifications. However, it is not guaranteed that all clades could be appropriately delimited by a robust set of morphological synapomorphies, given that many of these other traits also seem to have evolved independently many times in *Mimosa*.

The emphasis in this study is on taxon rather than character sampling to ensure adequate taxonomic and geographic coverage for such a species-rich group. The trade-off for this is reliance on a single plastid locus. It has been shown that adding more taxa to phylogenies can improve accuracy of phylogenetic estimates (Graybeal, 1998; Hillis, 1998), and for *Mimosa*, *trnD-trnT* provides enough informative data to construct a reasonably well-resolved and robustly supported gene tree. However, there can be many reasons why gene trees based on one or a few loci fail to reflect the evolutionary relationships among species. Issues related to horizontal gene transfer, hybridization, reticulation, incomplete lineage-sorting, paralogous genes, and pseudogenes, can all contribute to gene tree–species tree incongruence (Doyle, 1997; Maddison, 1997). Therefore, sequencing of biparentally inherited nuclear genes will be needed to confirm the relationships presented here, especially given the existence of a significant number of known polyploids and putative hybrids in the genus (Seijo and Fernandez, 2001; Morales et al., 2010; Dahmer et al., 2011).

Biogeography and dating analysis—A general result found here is the strong geographical structuring of the phylogeny, in which species in any particular clade tend to occur in the same biogeographical region. Examples are clade B (USA, Mexico, and Mesoamerica), clades C and W (Andes), clade E (Old World), clade I (northeast Brazil), clade K (southern South America), clades O and R (central Brazil), clade V (Mexico) and clade X (subtropical South America) (Fig. 1). In many instances, species previously regarded as taxonomically distantly related were placed in the same biogeographically coherent clade.

Geography has been found to be an important predictor of phylogenetic structure, particularly across the diverse seasonally dry tropical forest plant groups that make up the so-called succulent biome (sensu Schrire et al., 2005). This structure has been attributed to phylogenetic niche conservatism (Donoghue, 2008), dispersal limitation, and in situ speciation within individual geographical areas (Schrire et al., 2009; Pennington et al., 2006, 2009). For example, previous studies have shown that phylogenies of typical phylogenetically niche conserved tropical dry forest plant groups such as *Coursetia*, *Poissonia* (Leguminosae), and *Ruprechtia* (Polygonaceae) have high levels of phylogenetic geographic structure (Lavin, 2006; Pennington et al., 2006; Queiroz and Lavin, 2011). A similar pattern of strong geographic structure in *Mimosa* has been found in the predominantly seasonally tropical dry forest clades, including southern Mexico dry forests (clade V), Andean dry valleys (clades C and W), and Caatinga in northeast Brazil (clade I) and Madagascar (clade E), suggesting that endemic lineages confined to each of these dry forest areas have persisted in relative isolation for several million years and that dispersal between highly disjunct fragments of tropical dry forest has been limited (Pennington et al., 2006).

Unlike these predominantly dry forest groups, *Mimosa* is also diverse in other neotropical biomes, thereby offering the opportunity for more detailed investigations of the role of ecology/geography on the structuring of phylogenies and to provide insights into the timing of origin and evolution of different biomes. For example, *Mimosa* lineages have been used as a source of phylogenetic evidence to investigate the evolutionary history of several prominent biomes in the noetropics, such as the Cerrado (several clades; Simon et al., 2009), the Amazon (clade A; Hoorn et al., 2010), and the Andes (clades A, C, and W; Pennington et al., 2010).

The time-calibrated phylogeny of *Mimosa* suggests a gradual accumulation of major lineages from 15 to 3 Ma (Fig. 4; online Appendix S5). Although not used in the dating analysis as constraints, putative *Mimosa* fossils described from the Oligocene

TABLE 3. Levels of homoplasy of six morphological characters mapped onto a molecular phylogeny of *Mimosa*, as measured by number of estimated steps and consistency (CI) and retention (RI) indices. See also Figs. 2 and 3.

Character	Steps	CI	RI
Petiolar nectary	1	1.00	1.00
Inflorescence type	24	0.04	0.55
Number of stamens	6	0.33	0.95
Number of petals	19	0.11	0.80
Pollen type	7	0.42	0.94
Sensitive leaves	8	0.12	0.50

of Mexico (Magallón-Puebla and Cevallos-Ferriz, 1994; Calvillo-Canadell and Cevallos-Ferriz, 2005) are compatible with the time frame estimated for the evolution of genus (*Mimosa* stem node 28 Ma; Simon et al., 2009). The rate of nucleotide substitution varied across the tree and deviated from a constant rate (BEAST parameter ucld.stdev = 0.66 [0.54–0.79], mean and 95% credibility interval), indicating significant branch rate heterogeneity among lineages. Particularly high substitution rates were observed in *M. strigillosa* (clade J) (Fig. 4).

Old world clade—Divergence time estimates for the lineage that gave rise to the Old World species indicate that *Mimosa* was established in that region during the late Miocene. The fact that the Old World clade is nested within a predominantly South American clade (Fig. 1) suggests that the ancestral area of the Old World mimosas could have been in South America. The ages estimated for the Old World clade (crown node 6.3 Ma, stem node 10.0 Ma, Fig. 4) are much too young to support any hypothesis involving continental vicariance between Africa and South America, since the initial split between these continents occurred ca. 100 Ma, with putative later connections, including the Early Tertiary North Atlantic land bridge and the Walvis Ridge, a possible Oligocene filter barrier linking Africa and South America (Tiffney, 1985; Morley, 2003), also significantly predating the late Miocene divergence time estimates for Old World *Mimosa*. This suggests that long-distance dispersal provides the most plausible explanation for this remarkable disjunction, in line with predominantly Miocene divergence time estimates for the majority of intracontinental and transcontinental crown groups in legumes (Lavin et al., 2004). Among the South American members of clade D, there is an intriguing suite of coastal species (e.g., *M. bimucronata*, which is abundant in coastal Brazil), which reinforces the hypothesis of a trans-Atlantic dispersal as the likely route for migration to the Old World. However, lack of resolution at the base of clades D and E precludes more precise inference about the exact ancestral area of the Old World clade within the neotropics or about where *Mimosa* first arrived in the Old World.

One unresolved question is why *Mimosa* is so poorly represented in continental Africa compared to the extraordinary species diversity found in South America, considering that both continents share similar climates and vegetation types. One possible explanation is that there has not been enough time since the arrival of *Mimosa* in the Old World for significant diversification to have occurred in Africa. However, this seems unlikely, as many younger *Mimosa* clades have diversified very extensively in the New World within a short time span. Another possibility could be widespread extinction of *Mimosa* lineages following an initial diversification in Africa or that possible niches available for *Mimosa* on that continent were already occupied by other taxa, pre-empting a major diversification of *Mimosa* in Africa.

In contrast to the paucity of species in east Africa, *Mimosa* is impressively diverse in Madagascar, with more than 30 species, the vast majority of them endemic (Villiers, 2002). Among the native species, only *M. latispinosa* extends to Africa and other islands in the Indian Ocean, but some of these could be recent introductions (Villiers, 2002). Because of lack of resolution among the African, Asian, and Malagasy clades, the present *Mimosa* phylogeny sheds no light on possible biogeographical or evolutionary scenarios for the diversification of the Old World species and whether the Malagasy mimosas came from Africa, which is the most frequent sister clade relationship for Malagasy groups (Yoder and Nowak, 2006), or from somewhere else. If this is the case in *Mimosa*, the imbalance in sister clades between continental Africa and Madagascar in terms of species richness observed here, would be in line with what has been found for some other groups of plants (e.g., Janssen et al., 2008).

Legume groups across all three subfamilies, including the *Chapmannia–Diphysa–Ormocarpum* group, the subtribe Phaseolinae, the *Dichrostachys*/*Calliandropsis* clade, and the *Delonix–Lemuropisum*/*Conzattia–Heteroflorum*, *Parkinsonia*, and *Haematoxylon* clades of the *Peltophorum* group, show similar disjunct distributions and sister group relationships between Madagascar/east Africa and the neotropics (Lavin and Luckow, 1993; Lavin et al., 2000, 2004; Thulin et al., 2004; Haston et al., 2005; Schrire et al., 2005). Some of these distributions have been discussed in relation to the boreotropics hypothesis, which predicts that some plant lineages used to be more widespread in the northern hemisphere spanning the north Atlantic and occupying land connections during the Eocene or early Oligocene, and consequently linking the floras of different continents (Wolfe, 1975; Lavin and Luckow, 1993; Schrire et al., 2003). According to this hypothesis, the present peculiar disjunct distributions of these taxa could be explained by the extinction of members of these lineages in most of the former range, which is supported by the occurrence of tropical fossil taxa in the Tertiary of North America and Europe. However, the younger ages estimated for the disjunction between Old World and neotropical lineages of *Mimosa* and the possible sister group relationship between South American elements and the Old World clade would not seem to support a boreotropical explanation in this case. Instead, long-distance oceanic dispersal, which has been proposed to explain several intercontinental disjunctions in many legume and other plant groups (e.g., Lavin et al., 2004; Renner, 2004), is more likely.

Conclusions—This study presents a major step toward the construction of a molecular phylogeny for the large and complex legume genus *Mimosa*. One of the strengths of the present analysis is the extensive taxon sampling, which establishes an overall phylogenetic framework for *Mimosa* in terms of morphological evolution and relationships. Many of the informal clades identified here prompt taxonomic recognition, which could eventually culminate in an updated infrageneric classification of the genus. However, it may not be entirely straightforward to directly translate a phylogeny into a classification. Potential obstacles for a new classification for *Mimosa* are the lack of diagnostic morphological apomorphies for some well-supported groups, the difficulties of implementing a strictly

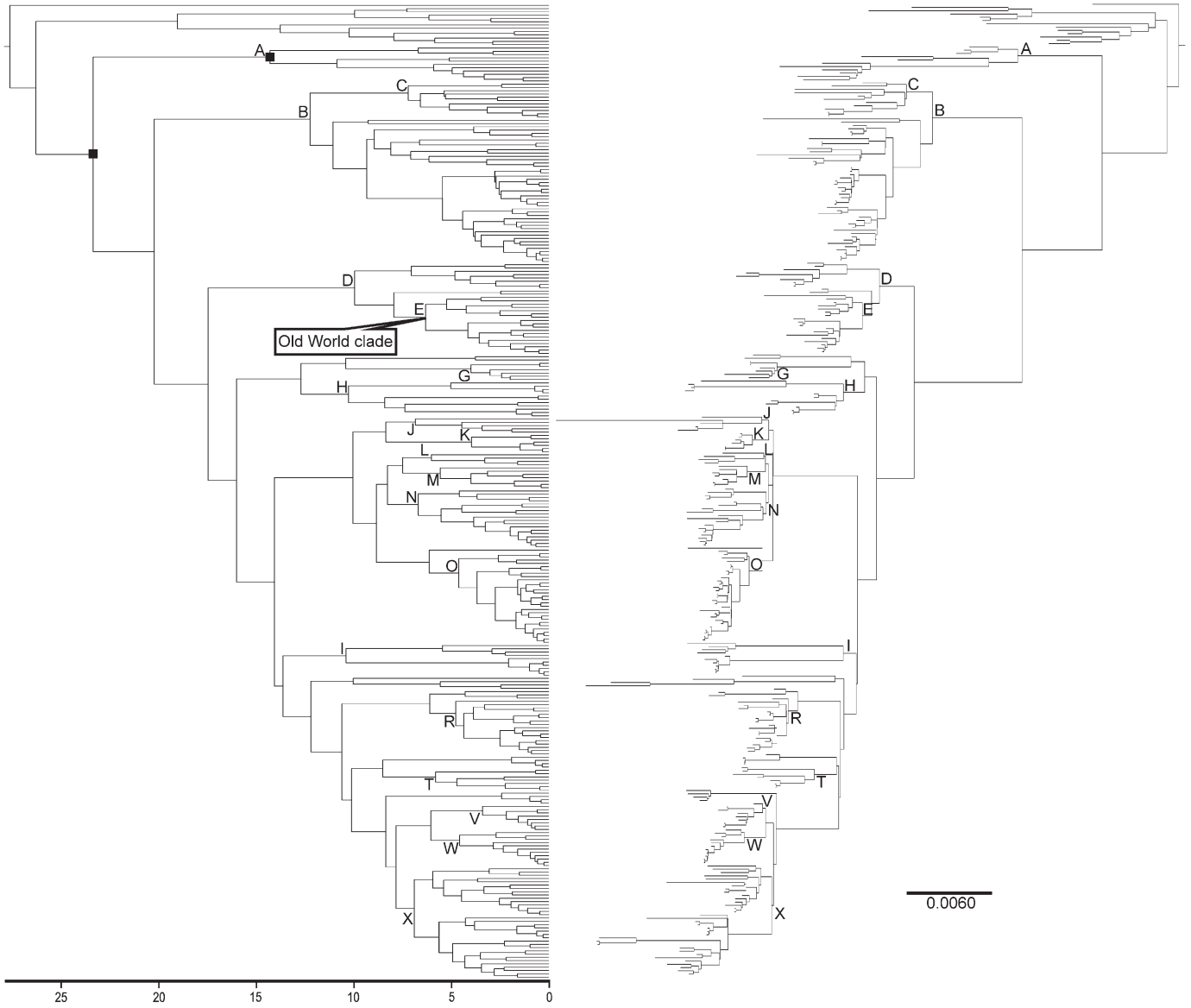

Fig. 4. Chronogram (left) derived from the *trnD-trnT* Bayesian dating analysis using an uncorrelated relaxed molecular clock (maximum credibility tree with averaged node ages across a set of 1000 Bayesian trees sampled at stationarity), and the corresponding phylogram (right). Letters are major clades discussed in the text, and squares are calibration points used in the analysis (*Mimosa* crown node and section *Mimadenia* crown node). Scale in million years (chronogram) and substitutions per site (phylogram).

rank-based classification following the Linnean system, the incomplete taxon sampling in the present analysis, which makes placement of unsampled species tentative, and the limited data set from a uniparentally inherited genome.

The affinities of the Old World species, which were not formally assessed in the most recent revision of *Mimosa* (Barneby, 1991), are explicitly analyzed for the first time, suggesting a late Miocene transoceanic dispersal from South America. The importance of geography and ecology, rather than morphology, in predicting many of the major groups within *Mimosa* is one of the most striking findings. In many cases, morphologically heterogeneous species grouped in robustly supported clades that can only be understood when geography is taken into account. The presence of some morphologically disparate species in well-supported clades implies strong geographic structure and extensive morphological homoplasy, suggesting that particular traits evolved independently several times in different groups. Another possibility, given that these results are based on a maternally inherited plastid gene tree, is that hybridization (including allopolyploidy) could have facilitated chlorolplast introgression, thereby generating an exaggerated impression of the extent of trans-specific geographic structure and potentially causing the erroneous inference of widespread homoplasy. Nevertheless, there are no indications of this type of conflict in our data set, since the known polyploids sampled here (27 species) are placed within morphologically homogeneous clades. In any case, the results presented here provide the essential foundations for disentangling potentially reticulate from divergent relationships, as well as a good interim working framework for comparative studies across the genus as a whole.

Finally, this paper illustrates how evolutionary patterns can emerge from the study of large and geographically widespread genera, as revealed here by geographical structuring and long-distance dispersal events. It also provides an example of how molecular phylogenies can illuminate the interpretation of morphological evolution, by reducing the subjectivity and controversy inherent to morphology-based classifications and providing robust phylogenetic foundations for classification of large and complex plant groups such as *Mimosa*. However, questions remain about the extent to which robustly supported monophyly and diagnosability can be applied to translate phylogenies into Linnean classifications.

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APPENDIX 1. Voucher information and GenBank accession numbers for taxa used in this study. Voucher specimens are deposited in the following herbaria: CEN = Embrapa Recursos Genéticos e Biotecnologia; E = Royal Botanic Garden, Edinburgh; FHO = University of Oxford; HUEFS = Universidade Estadual de Feira de Santana; ICN = Universidade Federal do Rio Grande do Sul; K = Royal Botanic Gardens, Kew; MEXU = Universidad Nacional Autónoma de México; MO = Missouri Botanical Garden; NY = New York Botanical Garden; RB = Jardim Botânico do Rio de Janeiro; UAMIZ = Universidad Autónoma Metropolitana, Iztapalapa; UB = Universidade de Brasília; VIC = Universidade Federal de Viçosa.

Section (given only for *Mimosa* species; Old World taxa were considered as belonging to section *Batocaulon*)—***Taxon***, *Voucher specimen*, Collection country, herbarium, GenBank accessions.

OUTGROUPS

Anadenanthera colubrina (Vell.) Brenan, *Hughes 2308*, Bolivia, FHO, FJ981975; ***Microlobius foetidus*** (Jacq.) M.Sousa & G.Andrade, *Hughes 2150*, Mexico, FHO, FJ981976; ***Parapiptadenia excelsa*** (Griseb.) Burkart, *Hughes 2425*, Bolivia, FHO, FJ982235; ***Piptadenia adiantoides*** (Spreng.) Macbride, *Simon 726*, Brazil, FHO, FJ982236; ***P. buchtienii*** Barneby, *Hughes 2427*, Bolivia, FHO, FJ982237; ***P. gonoacantha*** (Mart.) Macbride, *Simon 735*, Brazil, FHO, FJ982238; ***P. stipulacea*** (Benth.) Ducke, *Simon 702*, Brazil, FHO, FJ982239; ***P. trisperma*** (Vell.) Benth., *Armstrong 512*, Brazil, FHO, FJ982240; ***P. viridiflora*** Benth., *Hughes 1681*, Mexico, FHO, FJ982241; ***Pityrocarpa moniliformis*** Benth., *Way SWM2449*, Brazil, K, FJ982242; ***P. obliqua*** Macbride, *Macqueen 439*, Mexico, K, FJ982243; ***Stryphnodendron adstringens*** (Mart.) Coville, *Simon 734*, Brazil, FHO, FJ982244; ***S. obovatum*** Benth., *Hughes 2397*, Bolivia, FHO, FJ982245.

Batocaulon—Mimosa acantholoba (Willd.) Poir. **var.** ***acantholoba***, *Eastwood 118*, Peru, FHO, FJ981977; ***M. acantholoba*** Poir. **var.** ***eurycarpa*** (B.L.Rob.) Barneby, *Montaño-Arias 28*, Mexico, UAMIZ, FJ981978; ***M. aculeaticarpa*** Ortega, *Simon 808*, Mexico, MEXU, FJ981980; ***M. acutistipula*** Benth. **var.** ***acutistipula***, *Simon 705*, Brazil, FHO, FJ981981; ***M. adenantheroides*** (Martens & Galleotti) Benth., *Martínez-Bernal 945*, Mexico, UAMIZ, FJ981982; ***M. adenantheroides*** (Martens & Galleotti) Benth. **var.** ***hystricosa*** (Brandegee) R.Grether, ined., *Tenorio 21201*, Mexico, MEXU, FJ981983; ***M. adenocarpa*** Benth., *Simon 728*, Brazil, FHO, FJ981984; ***M. adenophylla*** Taub. ex Glaz., *Simon 458*, Brazil, UB, FJ981985; ***M. adenophylla*** Taub. ex Glaz. **var.** ***mitis*** Barneby, *Lima 184*, Brazil, HUEFS, FJ981986; ***M.*** **aff.** ***dalyi*** Barneby, *Wood 24306*, Bolivia, K, JF694256; ***M.*** **aff.** ***weberbaueri*** Harms, *Pennington 17903*, Peru, K, FJ981990; ***M. andina*** Benth., *Lewis 2271*, Ecuador, K, HM353071; ***M. antioquensis*** Killip ex Rudd **var.** ***isthmensis*** R.Grether, *Simon 860*, Mexico, MEXU, FJ981995; ***M. apodocarpa*** Benth., *Simon 635*, Brazil, UB, FJ981997; ***M. arenosa*** (Willd.) Poir. **var.** ***leiocarpa*** (DC.) Barneby, *Martínez-Bernal 923*, Mexico, UAMIZ, FJ981998; ***M. artemisiana*** Heringer & Paula, *Faria 138*, Brazil, RB, FJ981999; ***M. aspera*** M.E.Jones, *Simon 817*, Mexico, MEXU, FJ982000; ***M. auriculata*** Benth., *Hughes 2405*, Bolivia, FHO, FJ982002; ***M. bahamensis*** Benth., *Way 132*, Mexico, K, FJ982003; ***M. benthamii*** Macbride, *Simon 848*, Mexico, MEXU, FJ982004; ***M. bifurca*** Benth., *Dahmer 4*, Brazil, ICN, FJ982005; ***M. bimucronata*** Kuntze, *Simon 301*, Brazil, UB, FJ982006; ***M. biuncifera*** Benth., *Simon 805*, Mexico, MEXU, FJ982007; ***M. blanchetii*** Benth., *Simon 688*, Brazil, FHO, FJ982008; ***M. borealis*** A.Gray, *Simon 873*, USA, FHO, FJ982010; ***M. busseana*** Harms, *Clarke 26*, Tanzania, K, FJ982013; ***M. caduca*** (Willd.) Poir., *Lewis 3006*, Ecuador, K, HM353080; ***M. caesalpiniifolia*** Benth., *Simon 756*, Brazil, FHO, FJ982014; ***M. calcicola*** B.L.Rob., *Simon 846*, Mexico, MEXU, FJ982015; ***M. campicola*** Harms **var.** ***planipes*** Barneby, *Simon 692*, Brazil, FHO, FJ982018; ***M. candollei*** R.Grether, *Hughes 2394*, Bolivia, FHO, FJ982020; ***M. ceratonia*** L. **var.** ***ceratonia***, *Grimes 3223*, Puerto Rico, NY, JF694259; ***M. ceratonia*** L. **var.** ***interior*** Barneby, *Simon 727*, Brazil, FHO, FJ982022; ***M. cordistipula*** Benth., *Simon 693*, Brazil, FHO, FJ982029; ***M. coruscocaesia*** Barneby, *Martins 469*, Brazil, UB, FJ982030; ***M. corynadenia*** Britton & Rose, *Sousa 12896*, Mexico, MEXU, FJ982031; ***M. costenya*** McVaugh, *Simon 833*, Mexico, MEXU, FJ982032; ***M. craspedisetosa*** R.H.Fortunato & R.Palese, *Wood 24488*, Bolivia, K, JF694260; ***M. cruenta*** Benth., *Queiroz 12575*, Brazil, HUEFS, FJ982033; ***M. crumenarioides*** L.P.Queiroz & G.P.Lewis, *Simon 722*, Brazil, FHO, FJ982034; ***M. dalyi*** Barneby, *Wood 16487*, Bolivia, K, FJ982039; ***M. delicatula*** Baill., *Sutherland 262*, Madagascar, K, FJ982043; ***M. depauperata*** Benth., *Simon 801*, Mexico, MEXU, FJ982045; ***M. detinens*** Benth., *Sanchez 46*, Bolivia, MO, FJ982046; ***M. diplotricha*** C.Wright ex Sauvalle **var.** ***diplotricha***, *Simon 877*, Taiwan, FHO, FJ982050; ***M. diplotricha*** C. Wright ex Sauvalle **var.** ***diplotricha***, *Simon 600*, Brazil, UB, FJ982049; ***M. distachya*** Cav. **var.** ***oligacantha*** (DC.) Barneby, *Ku 365*, Mexico, MEXU, FJ982052; ***M. domingensis*** Benth., *Barneby 18276*, Dominican Republic, NY, FJ982055; ***M. dysocarpa*** Benth., *Newman 296*, USA, K, FJ982059; ***M. echinocaula*** Benth., *Simon 679*, Brazil, UB, FJ982060; ***M. emoryana*** Benth., *Grether 2842*, Mexico, UAMIZ, FJ982061; ***M. ervendbergii*** A.Gray, *Martínez 35132*, Mexico, MEXU, FJ982062; ***M. farinosa*** Griseb., *Wood 21535*, Bolivia, K, HM353086; ***M. filipes*** Mart., *Queiroz 10058*, Brazil, HUEFS, FJ982065; ***M. galeottii*** Benth., *Simon 840*, Mexico, MEXU, FJ982069; ***M. gatesiae*** Barneby, *Simon 741*, Brazil, FHO, FJ982070; ***M. gemmulata*** Barneby **var.** ***gemmulata***, *Simon 690*, Brazil, FHO, FJ982071; ***M. gracilis*** Benth. **var.** ***invisiformis*** Barneby, *Simon 762*, Brazil, FHO, FJ982073; ***M. gracilis*** Benth. **var.** ***stipitata*** Barneby, *Simon 745*, Brazil, FHO, FJ982074; ***M. grandidieri*** Baill., *Du Puy M56*, Madagascar, K, FJ982075; ***M. guaranitica*** Chodat & Hassl., *Nascimento 474*, Brazil, HUEFS, FJ982076; ***M. guatemalensis*** (Hook. & Arn.) Benth., *Simon 831*, Mexico, MEXU, FJ982077; ***M. hafomantsina*** Villiers, *Lewis 2138*, Madagascar, K, FJ982080; ***M. hamata*** Willd., *Simon 876*, India, FHO, FJ982081; ***M. hexandra*** M.Micheli, *Simon 711*, Brazil, FHO, FJ982084; ***M. hexandra*** M.Micheli, *Fabian-Martinez 128*, Mexico, MEXU, FJ982083; ***M. hondurana*** Britton, *Simon 858*, Mexico, MEXU, FJ982087; ***M. interrupta*** Benth., *Queiroz 10485*, Brazil, HUEFS, FJ982093; ***M. interrupta*** Benth., *Queiroz 10584*, Brazil, HUEFS, JF694262; ***M. invisa*** Mart. ex Colla **var.** ***invisa***, *Simon 715*, Brazil, FHO, FJ982094; ***M. jaenensis*** T.E.Särkinen, J.L.Marcelo-Peña & C.E.Hughes, *Särkinen 3070*, Peru, FHO, HM353091; ***M. lacerata*** Rose, *Hughes 2057*, Mexico, FHO, FJ982099; ***M. laticifera*** Rizzini & Mattos, *Simon 599*, Brazil, UB, FJ982104; ***M. latispinosa*** Lam., *Sutherland 206*, Madagascar, K, FJ982105; ***M. lepidota*** Herzog, *Hughes 2469*, Bolivia, FHO, FJ982107; ***M. leptantha*** Benth., *Nascimento 471*, Brazil, HUEFS, FJ982108; ***M. leptocarpa*** Rose, *Rico 1014*, Mexico, K, FJ982109; ***M. leucaenoides*** Benth., *Montaño-Arias 8*, Mexico, UAMIZ, FJ982110; ***M. levenensis*** Drake, *Luckow 4453*, Madagascar, FHO, FJ982111; ***M. lewisii*** Barneby, *Simon 696*, Brazil, FHO, FJ982112; ***M. luisana*** Brandegee, *Simon 844*, Mexico, FHO, FJ982114; ***M. malacophylla*** A.Gray, *Camargo-Ricalde 530*, Mexico, UAMIZ, FJ982115; ***M. martindelcampoi*** Medrano, *Camargo-Ricalde 527*, Mexico, UAMIZ, FJ982117; ***M. menabeensis*** R. Vig. **var.** ***menabeensis***, *Sutherland 209*, Madagascar, K, FJ982119; ***M. minarum*** Barneby, *Nascimento 495*, Brazil, HUEFS, FJ982120; ***M. minutifolia*** B.L.Rob. & Greenm., *Simon 810*, Mexico, MEXU, FJ982121; ***M. misera*** Benth., *Simon 703*, Brazil, FHO, JF694264; ***M. mollis*** Benth., *Simon 850*, Mexico, MEXU, FJ982123; ***M. monancistra*** Benth., *Simon 809*, Mexico, MEXU, FJ982124; ***M. montana*** Kunth. **var.** ***montana***, *Hughes 2225*, Peru, FHO, FJ982125; ***M. montana*** Kunth. **var.** ***sandemanii*** Barneby, *Eastwood 125*, Peru, FHO, HM353099; ***M. morroensis*** Barneby, *Nascimento 244*, Brazil, HUEFS, JF694266; ***M. mossambicensis*** Brenan, *Brummitt 8896*, Malawi, K, FJ982126; ***M. myriocephala*** Baker, *Rakoto 329*, Madagascar, K, FJ982128; ***M. nanchititlana*** R.Grether & Barneby, *Grether 2938*, Mexico, UAMIZ, FJ982129; ***M. nossibiensis*** Benth. **var.** ***nossibiensis***, *Du Puy M350*, Madagascar, K, FJ982131; ***M. nuttallii*** (DC.) B.L.Turner, *Simon 875*, USA, FHO, FJ982134; ***M. onilahensis*** R.Vig., *Du Puy M899*, Madagascar, K, FJ982138; ***M. ophthalmocentra*** Mart. ex Benth., *Way SWM2434*, Brazil, K, FJ982139; ***M. orthocarpa*** Spruce ex Benth., *Simon 855*, Mexico, MEXU, FJ982141; ***M. palmeri*** Rose, *Simon 823*, Mexico, MEXU, FJ982142; ***M. paucifolia*** Benth., *Dutra 450*, Brazil, VIC, JF694268; ***M. platycarpa*** Benth. **var.** ***platycarpa***, *Simon 859*, Mexico, MEXU, FJ982152; ***M. polyantha*** Benth., *Simon 829*, Mexico, MEXU, FJ982153; ***M. polydidyma*** Barneby, *Simon 719*, Brazil, FHO, FJ982157; ***M. prainiana*** Gamble, *Maesen 3834*, India, K, FJ982158; ***M. pseudosepiaria*** Harms, *Simon 712*, Brazil, FHO, FJ982161; ***M. psoralea*** Benth., *Phillipson 3571*, Madagascar, K, FJ982164; ***M. pteridifolia*** Benth., *Simon 754*, Brazil, FHO, FJ982165; ***M. purpusii*** Brandegee, *Simon 841*, Mexico, MEXU, FJ982167; ***M. quadrivalvis*** L. **var.** ***quadrivalvis***, *Camargo-Ricalde 532*, Mexico, UAMIZ, FJ982169;

M. quitensis Benth., *Lewis 2856*, Ecuador, K, HM353116; ***M. rhodocarpa*** (Britton & Rose) R.Grether, *Hughes 2161*, Mexico, FHO, FJ982175; ***M. robusta*** R.Grether, *Simon 818*, Mexico, MEXU, FJ982176; ***M. rubicaulis*** Lam. **subsp.** ***himalayana*** (Gamble) H.Ohashi, *Thomas 24/1*, Nepal, K, FJ982177; ***M. rupertiana*** B.L.Turner, *Bye 12884*, Mexico, MEXU, FJ982179; ***M. schomburgkii*** Benth., *Hellin 15*, Honduras, FHO, FJ982183; ***M. sericantha*** Benth., *Simon 410*, Brazil, UB, FJ982185; ***M. setuligera*** Harms, *Simon 709*, Brazil, FHO, FJ982189; ***M. similis*** Britton & Rose, *Simon 807*, Mexico, MEXU, FJ982191; ***M. sinaloensis*** Britton & Rose, *Simon 828*, Mexico, MEXU, FJ982192; ***M. spirocarpa*** Rose, *Simon 825*, Mexico, MEXU, FJ982198; ***M. strobiliflora*** Burkart, *Ribas 3600*, Brazil, HUEFS, FJ982202; ***M. tejupilcana*** R.Grether & A.Martínez-Bernal, *Montaño-Arias 16*, Mexico, UAMIZ, FJ982204; ***M. tenuiflora*** (Willd.) Poir., *Simon 698*, Brazil, FHO, FJ982205; ***M. texana*** Small **var.** ***filipes*** (Britton & Rose) Barneby, *Simon 845*, Mexico, MEXU, FJ982207; ***M. texana*** Small **var.** ***texana***, *Simon 803*, Mexico, MEXU, FJ982208; ***M. torresiae*** R.Grether, *Torres-Colin 10040*, Mexico, MEXU, FJ982209; ***M. ulbrichiana*** Harms, *Simon 710*, Brazil, FHO, FJ982212; ***M. uliginosa*** Chod. & Hassl., *Queiroz 12608*, Brazil, HUEFS, FJ982214; ***M. unipinnata*** B.D.Parfitt & Pinkava, *Carranza 2355*, Mexico, MEXU, FJ982215; ***M. uraguensis*** Hook. & Arn., *Simon 862*, cultivated, FHO, FJ982216; ***M. verrucosa*** Benth., *Simon 706*, Brazil, FHO, FJ982221; ***M. vilersii*** Drake, *Labat 3020*, Madagascar, K, FJ982223; ***M. volubilis*** Villiers, *Du Puy M739*, Madagascar, K, FJ982226; ***M. waterlotii*** R.Vig., *Schrire 2551*, Madagascar, K, FJ982227; ***M. weberbaueri*** Harms, *Hughes 2043*, Peru, FHO, FJ982229; ***M. xavantinae*** Barneby, *Farias 346*, Brazil, UB, FJ982233; ***M. xiquexiquensis*** Barneby, *Harley 54331*, Brazil, HUEFS, JF694271; ***M. zygophylla*** Benth., *Camargo-Ricalde 525*, Mexico, UAMIZ, FJ982234.

Calothamnos—Mimosa **aff.** ***bathyrrhena*** Barneby, *Simon 874*, Brazil, FHO, FJ981988; ***M. aurivillus*** Mart. **var.** ***aurivillus***, *Dutra 348*, Brazil, VIC, JF694257; ***M. aurivillus*** Mart. **var.** ***calothamnos*** (Benth.) Barneby, *Dutra 347*, Brazil, VIC, JF694258; ***M. daleoides*** Benth., *Schinini 35683*, Argentina, MEXU, FJ982038; ***M. flocculosa*** Burkart, *CNPF sn*, Brazil,–, FJ982067; ***M. incana*** Benth., *Dahmer 2*, Brazil, ICN, FJ982091; ***M. leprosa*** (Benth.) Macbride **var.** ***parviceps*** Barneby, *Dutra 358*, Brazil, VIC, JF694263; ***M. pilulifera*** Benth., *Dahmer 3*, Brazil, ICN, FJ982149; ***M. pilulifera*** Benth. **var.** ***pseudincana*** (Burkart) Barneby, *Simon 878*, Brazil, FHO, FJ982150; ***M. scabrella*** Benth., *Lima 4055*, Brazil, RB, FJ982181.

Habbasia—Mimosa adenotricha Benth., *Dutra 332*, Brazil, VIC, FJ981987; ***M. albolanata*** Taub. **var.** ***paucipinna*** (Benth.) Barneby, *Simon 667*, Brazil, UB, FJ981994; ***M. antrorsa*** Benth., *Fagg 1747*, Brazil, UB, FJ981996; ***M. brachycarpa*** Benth., *Queiroz 10589*, Brazil, HUEFS, FJ982011; ***M. camporum*** Benth., *Faria 729*, Brazil, RB, FJ982019; ***M. cisparanensis*** Barneby, *Simon 568*, Brazil, UB, FJ982024; ***M. claussenii*** Benth. **var.** ***claviceps*** Barneby, *Simon 766*, Brazil, FHO, FJ982025; ***M. claussenii*** Benth. **var.** ***megistophylla*** Barneby, *Simon 768*, Brazil, FHO, FJ982026; ***M. cryptothamnos*** Barneby, *Simon 738*, Brazil, FHO, FJ982035; ***M. decorticans*** Barneby, *Simon 681*, Brazil, UB, FJ982042; ***M. densa*** Benth. **var.** ***densa***, *Simon 870*, Brazil, FHO, FJ982044; ***M. diminuta*** M.F.Simon & C.E.Hughes, *Simon 866A*, Brazil, FHO, FJ982048; ***M. dominarum*** Barneby, *Simon 776*, Brazil, FHO, FJ982054; ***M. dormiens*** Humb. & Bonpl. ex Willd., *Guadarrama 6841*, Mexico, MEXU, FJ982056; ***M. foliolosa*** Benth. **var.** ***pubescens*** Benth., *Simon 733*, Brazil, FHO, FJ982068; ***M. heringeri*** Barneby, *Proença 2138*, Brazil, UB, FJ982082; ***M. humivagans*** Barneby, *Simon 737*, Brazil, FHO, FJ982089; ***M. josephina*** Barneby, *Hughes 2398*, Bolivia, FHO, FJ982097; ***M. kalunga*** M.F.Simon & C.E.Hughes, *Simon 866*, Brazil, FHO, FJ982098; ***M. laniceps*** Barneby, *Simon 773*, Brazil, FHO, FJ982102; ***M. manidea*** Barneby, *Simon 760*, Brazil, FHO, FJ982116; ***M. melanocarpa*** Benth., *Simon 675*, Brazil, UB, FJ982118; ***M. neptuniodes*** Harms, *Wood 22123*, Bolivia, K, FJ982130; ***M. occidentalis*** Britton & Rose, *Simon 821*, Mexico, MEXU, FJ982136; ***M. oligosperma*** Barneby, *Simon 865*, Brazil, FHO, FJ982137; ***M. pigra*** L. **var.** ***berlandieri*** (A.Gray) B.L.Turner, *Camargo-Ricalde 531*, Mexico, UAMIZ, FJ982147; ***M. pigra*** L. **var.** ***dehiscens*** (Barneby) D.Glazier & Mackinder, *Hughes 2414*, Bolivia, FHO, FJ982148; ***M. poculata*** Barneby, *Queiroz 10160*, Brazil, HUEFS, JF694269; ***M. pseudosetosa*** M.F.Simon & C.E.Hughes, *Simon 864*, Brazil, FHO, FJ982162; ***M. regina*** Barneby, *Simon 759*, Brazil, FHO, FJ982173; ***M. setosa*** Benth. **var.** ***paludosa*** (Benth.) Barneby, *Simon 725*, Brazil, FHO, FJ982186; ***M. setosa*** Benth. **var.** ***urbica*** Barneby, *Simon 730*, Brazil, FHO, FJ982187; ***M. setosissima*** Taub., *Simon 676*, Brazil, UB, FJ982188; ***M. somnians*** Humb. & Bonpl. ex Willd. **var.** ***lasiocarpa*** (Benth.) Barneby, *Simon 736*, Brazil, FHO, FJ982194; ***M. speciosissima*** Taub., *Simon 753*, Brazil, FHO, FJ982197; ***M. splendida*** Barneby, *Simon 739*, Brazil, FHO, FJ982199; ***M. strigillosa*** Torr. & A.Gray, *Lievens 2666*, USA, MEXU, FJ982201; ***M. stylosa*** Barneby, *Dutra 318*, Brazil, VIC, FJ982203; ***M. ulei*** Taub. **var.** ***grallator*** Barneby, *Simon 777*, Brazil, FHO, FJ982213; ***M. viperina*** M.F.Simon & C.E.Hughes, *Simon 461*, Brazil, FHO, FJ982224; ***M. weddelliana*** Benth., *Ritter 4604*, Bolivia, MO, FJ982230.

Mimadenia—Mimosa colombiana Britton & Killip, *Torres 21343*, Colombia, K, FJ982027; ***M. guilandinae*** (DC.) Barneby **var.** ***guilandinae***, *Prévost 3958*, French Guiana, K, FJ982078; ***M. irrigua*** Barneby, *Simon 694*, Brazil, FHO, FJ982095; ***M. lepidophora*** Rizzini, *Cardoso 1747*, Brazil, FHO, FJ982106; ***M. myriadenia*** (Benth.) Benth. **var.** ***punctulata*** (Benth.) Barneby, *Acevedó-Rdgz 7483*, Ecuador, K, FJ982127; ***M. nothacacia*** Barneby, *Lewis 2353*, Ecuador, K, FJ982132; ***M. pithecolobioides*** Benth., *Dutra 317*, Brazil, VIC, FJ982151; ***M. revoluta*** Benth., *Hughes 2278*, Bolivia, FHO, FJ982174; ***M. rufescens*** Benth. **var.** ***rufescens***, *Ferreira 596*, Brazil, K, FJ982178; ***M. townsendii*** Barneby, *Lewis 3025*, Ecuador, K, FJ982210; ***M. watsonii*** B.L.Rob., *Simon 857*, Mexico, MEXU, FJ982228.

Mimosa—Mimosa acapulcensis B.L.Rob., *Otero R2*, Mexico, MEXU, FJ981979; ***M. adamantina*** Barneby **var.** ***adamantina***, *Dutra 459*, Brazil, VIC, JF694255; ***M.*** **aff.** ***flagellaris*** Benth., *Queiroz 12322*, Brazil, HUEFS, FJ981989; ***M.*** **aff.** ***incarum*** Barneby, *Pennington 1715*, Peru, E, HM353081; ***M.*** **aff.** ***polycarpa*** Kunth **var.** ***polycarpa***, *Eastwood 89*, Peru, FHO, HM353082; ***M.*** **aff.** ***xanthocentra*** Mart., *Queiroz 10476*, Brazil, HUEFS, FJ981991; ***M. affinis*** B.L.Rob., *Simon 814*, Mexico, MEXU, FJ981992; ***M. albida*** Humb. & Bonpl. ex Willd. **var.** ***albida***, *Hughes 2083*, Mexico, FHO, FJ981993; ***M. atlantica*** Barneby, *Ribas 4333*, Brazil, HUEFS, FJ982001; ***M. boliviana*** Benth., *Hughes 2426*, Bolivia, FHO, FJ982009; ***M. brevipetiolata*** Burkart **var.** ***hirtula*** (Burkart) Barneby, *Queiroz 12614*, Brazil, HUEFS, FJ982012; ***M. callidryas*** Barneby, *Cruz 94*, Brazil, HUEFS, FJ982016; ***M. callithrix*** Malme, *Simon 684*, Brazil, UB, FJ982017; ***M. casta*** L., *Johnson 2189-80*, Panama, MEXU, FJ982021; ***M. chartostegia*** Barneby, *Ribas 5085*, Brazil, HUEFS, FJ982023; ***M. coniflora*** Burkart, *Ribas 3060*, Brazil, HUEFS, FJ982028; ***M. ctenodes*** Barneby, *Hughes 2212*, Peru, FHO, FJ982036; ***M. cyclophylla*** Taub., *Simon 757*, Brazil, FHO, FJ982037; ***M. deamii*** B.L.Rob., *Martínez-Bernal 919*, Mexico, UAMIZ, FJ982040; ***M. debilis*** Humb. & Bonpl. ex Willd. **var.** ***debilis***, *Hughes 2393*, Bolivia, FHO, FJ982041; ***M. dicerastes*** Barneby, *Simon 448*, Brazil, UB, FJ982047; ***M. discobola*** Barneby, *Simon 744*, Brazil, FHO, FJ982051; ***M. dolens*** Vell. **var.** ***dolens***, *Dutra 352*, Brazi, VIC, JF694261; ***M. dolens*** Vell. **var.** ***rigida*** (Benth.) Barneby, *Simon 879*, Brazil, FHO, FJ982053; ***M. dryandroides*** Taub. ex Glaz., *Ribas 3449*, Brazil, HUEFS, FJ982057; ***M. dutrae*** Malme, *Dahmer 5*, Brazil, ICN, FJ982058; ***M. fachinalensis*** Burkart, *Dahmer 16*, Brazil, ICN, FJ982063; ***M. fachinalensis*** Burkart, *Dahmer 20*, Brazil, ICN, FJ982064; ***M. flagellaris*** Benth., *Queiroz 12545*, Brazil, HUEFS, FJ982066; ***M. goldmanii*** B.L.Rob., *Martínez-Bernal 921*, Mexico, UAMIZ, FJ982072; ***M. gymnas*** Barneby, *Silva 3541*, Brazil, HUEFS, FJ982079; ***M. hirsutissima*** Mart. **var.** ***barbigera*** (Benth.) Barneby, *Simon 765*, Brazil, FHO, FJ982085; ***M. hirsutissima*** Mart. **var.** ***grossa*** Barneby, *Queiroz 12854*, Brazil, HUEFS, FJ982086; ***M. honesta*** Mart., *Simon 720*, Brazil, FHO, FJ982088; ***M. hypoglauca*** Mart. **var.** ***hypoglauca***, *Simon 723*, Brazil, FHO, FJ982090; ***M. incarum*** Barneby, *Hughes 2206*, Peru, FHO, FJ982092; ***M. jacobita*** Barneby, *Hughes 2400*, Bolivia, FHO, FJ982096; ***M. lactiflua*** Delile ex Benth., *Hughes 2079*, Mexico, FHO, FJ982100; ***M. lamolina*** C.E.Hughes & G.P.Lewis, *Hughes 2648*, Peru, FHO, FJ982101; ***M. lanuginosa*** Glaz. ex Burkart **var.** ***lanuginosa***, *Simon 732*, Brazil, FHO, FJ982103; ***M. loxensis*** Barneby, *Lewis 2987*, Ecuador, K, FJ982113; ***M. modesta*** Mart. **var.** ***modesta***, *Simon 708*, Brazil, FHO, FJ982122; ***M. montis-carasae*** Barneby, *Dutra 623*, Brazil, VIC, JF694265; ***M. nuda*** Benth. **var.** ***nuda***, *Hughes 2396*, Bolivia, FHO, FJ982133; ***M. oblonga*** Benth., *Barbosa 463*, Brazil, HUEFS, FJ982135; ***M. orthacantha*** Benth., *Barros sn*, Brazil, K, FJ982140; ***M. papposa*** Benth. **var.** ***papposa***, *Simon 601*, Brazil, UB, FJ982143; ***M. parviceps*** Barneby, *Dutra 437*, Brazil, VIC, JF694267; ***M. pectinatipinna*** Burkart, *Hughes 2036*, Peru, FHO, FJ982144; ***M. pedersenii*** Barneby, *Queiroz 12645*, Brazil, HUEFS, FJ982145; ***M. per-dusenii*** Burkart, *Ribas 4545*, Brazil, HUEFS, FJ982146; ***Mimosa*** **sp.**, *Hughes 2642*, Peru, FHO, HM353125; ***M. polycarpa*** Kunth **var.** ***subandina*** Barneby, *Hughes 2462*,

Bolivia, FHO, FJ982154; ***M. polycephala*** Benth. **var.** ***polycephala***, *Simon 400*, Brazil, UB, FJ982155; ***M. polydactyla*** Humb. & Bonpl. ex Willd., *Coradin 8682*, Brazil, CEN, FJ982156; ***M. pseudocallosa*** Burkart, *Ribas 5845*, Brazil, HUEFS, FJ982159; ***M. pseudoradula*** Glaz. ex Barneby **var.** ***pseudoradula***, *Simon 664*, Brazil, UB, FJ982160; ***M. psilocarpa*** B.L.Rob., *Martínez-Bernal 933*, Mexico, UAMIZ, FJ982163; ***M. pudica*** L., *Simon 669*, Brazil, UB, FJ982166; ***M. pyrenea*** Taub., *Simon 678*, Brazil, UB, FJ982168; ***M. radula*** Benth. **var.** ***imbricata*** (Benth.) Barneby, *Simon 731*, Brazil, FHO, FJ982170; ***M. ramboi*** Burkart, *Queiroz 12530*, Brazil, HUEFS, FJ982171; ***M. ramulosa*** Benth., *Queiroz 12340*, Brazil, HUEFS, FJ982172; ***M. rusbyana*** Barneby & Fortunato, *Särkinen 2071*, Bolivia, FHO, FJ982180; ***M. schleidenii*** Herter, *Queiroz 12348*, Brazil, HUEFS, FJ982182; ***M. sensitiva*** L. **var.** ***sensitiva***, *Almeida 4*, Brazil, HUEFS, FJ982184; ***M. sicyocarpa*** B.L.Rob., *Calóncio 4936*, Mexico, MEXU, FJ982190; ***M. skinneri*** Benth. **var.** ***desmodioides*** (Benth.) Barneby, *Simon 746*, Brazil, FHO, FJ982193; ***M. sousae*** R.Grether, *Martínez-Bernal 918*, Mexico, UAMIZ, FJ982195; ***Mimosa*** **sp.**, *Wood 23707*, Bolivia, K, JF694270; ***M. sparsiformis*** Barneby, *Dahmer 15*, Brazil, ICN, FJ982196; ***M. sprengelii*** DC., *Queiroz 12469*, Brazil, HUEFS, FJ982200; ***M. tequilana*** S.Watson, *Simon 813*, Mexico, MEXU, FJ982206; ***M. tricephala*** Cham. & Schltdl. **var.** ***nelsonii*** (B.L.Rob.) Chehaibar & R.Grether, *Martínez-Bernal 920*, Mexico, UAMIZ, FJ982211; ***M. ursina*** Mart., *Simon 704*, Brazil, FHO, FJ982217; ***M. velloziana*** Mart. **var.** ***velloziana***, *Simon 721*, Brazil, FHO, FJ982218; ***M. venatorum*** Barneby, *Simon 740*, Brazil, FHO, FJ982219; ***M. verecunda*** Benth., *Simon 749*, Brazil, FHO, FJ982220; ***M. vestita*** Benth., *Simon 769*, Brazil, FHO, FJ982222; ***M. virgula*** Barneby, *Silva 5134*, Brazil, UB, FJ982225; ***M. woodii*** Atahuachi & C.E.Hughes, *Hughes 2285*, Bolivia, FHO, FJ982231; ***M. xanthocentra*** Mart. **var.** ***subsericea*** (Benth.) Barneby, *Hughes 2403*, Bolivia, FHO, FJ982232.

APPENDIX 2. Circumscriptions of 24 well-supported clades (A–X) found in the phylogenetic analysis (Fig. 1).

Clade A is a robustly supported early-diverging group that is equivalent to Barneby's (1991) section *Mimadenia*, a group of 15 species, of which 11 were sampled here. This group retains the ancestral character state of extrafloral nectaries shared with piptadenioid sister genera (Fig. 2b), while across the rest of the genus the nectary has been reduced to a nonfunctional spicule or been lost entirely. In addition, species in section *Mimadenia* generally have more (up to 16) pollen grains per polyad, whereas the remaining species of *Mimosa* have polyads of eight or four grains (Fig. 3b). Clade A is further subdivided into two geographically and ecologically distinct subclades, one comprising Andean elements of mid-elevation seasonally dry ecology (*M. revoluta*, *M. townsendii* and *M. nothacacia*), and the other lowland species widespread across the neotropics, including a number of rain forest lianas, semi-arid thorn scrub, and savanna species (Fig. 1).

Clade B is a rather large and morphologically diverse clade containing around 65 species and brings together several series of section *Batocaulon*, including series *Dystachyae* (16 species), *Acanthocarpae* (13), *Acantholobae* (2), *Boreales* (10), *Leucaenoideae* (3), *Rubicaules* (4 excluding Old World species, but see Bentham, 1875), *Fagaracanthae* (7), *Bahamenses* (1), and *M. leptocarpa* (series *Plurijugae*), plus clade C. The clade comprises morphologically disparate elements that include convergent haplostemony in *M. leptocarpa* and *M. tejupilcana* (Fig. 2d), but is geographically well-defined with all species centered in the USA, Mexico, the Caribbean, and Central America, except for the predominantly South American clade C nested within (see below). None of the series represented in clade B, except *Acantholobae,* are monophyletic (Table 2). However, in some cases, lack of resolution and/or sparse taxon sampling preclude assessment of the monophyly of infrageneric groups. For example, series *Fagaracanthae*, an essentially Caribbean group rich in endemics, is represented by only one species (*M. domingensis*), and more samples are needed to confirm the affinity of this series to the Mexican species.

Clade C, nested within clade B, is a taxonomically heterogeneous group of around 10 species that combines members of three different series of section *Batocaulon* including series *Andinae* (5), *Bimucronatae* (*M. hexandra*), and *Farinosae* (*M. detinens*). The last two series are shown to be polyphyletic since some of their species are nested within clade D (see below). Clade C is likely to also include *M. ostenii*, which is morphologically similar to *M. detinens* in series *Farinosae* (Barneby, 1991) and also grows in lowlands in southern South America. The same would apply to *M. exalbescens*, which is the putative sibling of *M. hexandra* in series *Bimucronatae* where these are the only species with trimerous flowers (Barneby, 1991). This group comprises dry lowland species distributed across the Paraguay basin, the Chaco, northeast Brazil; dry-forests in Colombia, Venezuela, and Mexico; and members of the ecologically and geographically well-defined series *Andinae*, which includes a set of narrowly distributed endemics from low- to mid-elevation Andean dry tropical forests (Särkinen et al., 2011).

Clade D is formed by species of section *Batocaulon* series *Caesalpiniifoliae* (*M. caesalpiniifolia* and *M. laticifera*), *Ceratoniae* (*M. ceratonia*), *Leiocarpae* (in part), *Bimucronatae* (*M. bimucronata* and *M. pseudosepiaria*), and *Farinosae* (*M. farinosa*), with the Old World clade E (see below) nested within it. The well-supported subclade formed by *M. arenosa*, *M. acutistipula*, *M. bimucronata*, *M. pseudosepiaria*, *M. ophthalmocentra*, and *M. farinosa* is somewhat heterogeneous in terms of flower morphology, including species with flowers with 3 or 4 petals, and both spicate and globose inflorescences. This morphological diversity is reflected in Barneby's (1991) classification, in which these species are assigned to three different series based on flower and inflorescence characteristics. The nonmonophyletism of most series within clade D precludes an estimation of the number of species in this group.

Clade E includes all Old World *Mimosa* species sampled here (half of those currently known) nested within the neotropical clade D, suggesting a possible single dispersal event from the Americas to the Old World (see main text for further discussion). The Asian (*M. prainiana*, *M. rubicaulis*, and *M. hamata*) and continental African species (*M. mossambicensis* and *M. busseana*) form well-supported subclades within clade E. However, the relationships of these two groups to the Malagasy species, which make up the majority of the Old World species are uresolved and still unclear. Clade E is formed by a morphologically homogeneus group of species with inflorescences in capitula, tetramerous flowers, diplostemony, and presence of recurved aculei, although many of these characters are also shared with other members of clade D. The affinity of the Old World species to the South American members of clade D was unexpected, since they had been previously tentatively placed within series *Rubicaules* with *M. ervendbergii*, *M. malacophylla*, and *M. hondurana* (clade B) and *M. sinaloensis* (clade G) (Bentham, 1875; Barneby, 1991). The apparent morphological similarity between the Old World species and neotropical members of series *Rubicaules* appears to be an example of independent evolution of similar morphological features, which is fairly common in *Mimosa*.

Clade F corresponds in part to series *Plurijugae* and potentially contains four species, two of which were sampled here. This clade represents one of the five hypothesized transitions from ancestral diplostemonous to haplostemonous flowers in *Mimosa* (Fig. 2d). *Mimosa leptocarpa* and *M. tejupilcana*, previously assigned to series *Plurijugae* (Barneby, 1991; Grether and Martínez-Bernal, 1996), grouped within clade B, and therefore appear to have aquired haplostemony independently.

Clade G supports the monophyly of the morphologically unified series *Quadrivalves* (section *Batocaulon*) with the inclusion of a single species (*M. sinaloensis*) from series *Rubicaules.* This clade is defined by a herbaceous diffuse or humifuse growth habit, stem armature of serial aculei, and diplostemonous flowers with 5–6 petals and has a center of species diversity in southern USA and Mexico, with only one species extending to South America. The distinct, narrow, tetragonal, valvately dehiscent pod, in which the replum is as wide as or wider than the valves, is characteristic of some taxa and gave the name to this series. However, this is not a synapomorphy for this clade, since similar pods have been reported in other unrelated groups, and also because some taxa within series *Quadrivalves*, as well as *M. sinaloensis*, have pods that resemble

a conventional craspedium (Barneby, 1991). Barneby (1991) reduced the former genus *Schrankia* (= series *Quadrivalves*) to a single species, *M. quadrivalvis*, with 16 varieties. However, this delimitation has not been widely accepted, with subsequent recognition of several taxa placed within *M. quadrivalvis* as distinct species (Grether, 2000; Turner, 1994a, b).

Clade H comprises a taxonomically widespread set of species mostly endemic to the Cerrado biome in Brazil. The nine species sampled here represent four series of section *Batocaulon*, including series *Paucifoliatae* (17 species), *Campicolae* (3), *Filipedes* (6), and *Echinocaulae* (1), making a possible total of 27 species. Most of these species are functionally herbaceous fire-adapted Cerrado endemics that grow from a napiform xylopodium, but a few extend to coastal and southern Brazil, Venezuela, and Belize. One species, *M. diplotricha*, is a pantropical invasive weed, which is represented here by accessions from Brazil and Taiwan. Species with trimerous flowers corresponding to series *Campicolae* and *Filipedes* form a well-supported subgroup within clade H (Fig. 3a).

Clade I corresponds to series *Cordistipulae*, a morphologically well-defined group among the diplostemonous species characterized by trimerous flowers, absence of interpinnal spicules, and paraphyllidia (Barneby, 1991). The clade is particularly diverse in northeast Brazil, with one widespread species (*M. guaranitica*) occurring in southern South America and also disjunct in Mexico. Ten of the 13 known species were sampled here.

Clade J is equivalent to series *Habbasia* of Barneby (1991), a group of potentially 10 species (four sampled here) of mostly wet tropical and warm temperate lowlands. One species (*M. pigra*) is a widespread weed in tropical wetlands.

Clade K is congruent with series *Stipellares*, a group of 19 species that grow in open grasslands in subtropical South America, although sampling within this clade is rather sparse (six species). The clade is defined by the presence of a dilated paraphyllidium that simulates a minute leaflet at the base of the pinna (Barneby, 1991).

Clade L combines series *Bipinnatae* (12 species, only three sampled here) in section *Batocaulon* and *M. adenocarpa* from series *Glandulosae* section *Habbasia*. The clade is widespread in the neotropics, mostly in wetlands, and comprises some weedy species.

Clade M contains all four species of series *Neptunioideae*, series *Rojasianae* (one of three species sampled), and the monotypic series *Auriculatae*, making a total of eight species of herbs and shrubs that grow in open lowlands across the Neotropics, with a few species endemic to the savannas of Brazil and Bolivia. The placement of *M. auriculata* as sister to *M. josephina* is intriguing, since they are morphologically very distinct, but geographically adjacent (sometimes sympatric) local endemics from the Serrania de Chiquitos in eastern Bolivia. Barneby (1991) placed *M. auriculata* in a monotypic series in section *Batocaulon*, since he found no obvious close relative for this species. However, all the other species in this clade are from section *Habbasia*. The presence of broad striate stipules provides one trait shared by all members of this clade. The position of *M. orthocarpa* (series *Glandulosae*), as sister to this clade, is unexpected in terms of the striking morphological dissimilarity.

Clade N comprises most of series *Leiocarpae* (probably 21 species, 14 sampled here) along with *M. lewisii* (series *Bimucronatae*). These species are mainly shrubs and trees with spicate inflorescences (except *M. lewisii*) and glands on the leaflets, except *M. dalyi* and *M. lewisii*, although the latter has a glandular indumentum. The remaining species of series *Leiocarpae*, which lack leaflet glands and have white flowers, apart from *M. dayli*, are placed within clade D (see above). The molecular data does not support the hypothesis of Grether (2000) that the species of series *Dystachyae* (Mexican centered group) with spicate inflorescences should be incorporated into series *Leiocarpae*, which is mainly South American, since these two groups appear to be distantly related on the plastid gene tree. It would be interesting to include *M. puberula* in the analysis, as it is the only Mexican species included by Barneby (1991) in series *Leiocarpae*, to verify its placement in the phylogeny.

Clade O is a large clade, remarkably rich in life forms and taxa. It comprises Barneby's series *Setosae* and *Pachycarpae* with ca. 50 species, of which 26 were sampled here. Four recently described species (Simon et al., 2010) are included here. The plastid topology prompts incorporation of series *Setosae* into series *Pachycarpae*.The similarities between these two series were mentioned by Barneby (1991) and are further discussed in Simon et al. (2010). All species grow in the Cerrado, and the vast majority are highly specialized fire-adapted local endemics. The adaptive strategies and morphological innovations to withstand fire are strikingly diverse and include rosulate trees (with leaves crowded at the tips of the branches), thickened terminal branches, persistent stipules that protect the trunk from fire, and prostrate or wand-like, functionally herbaceous subshrubs growing from stout xylopodia (Simon et al., 2009).

Clade P is a small group comprising *M. pudica*, *M. polydactyla* (series *Mimosa*, subseries *Pudicae*), and *M. affinis* (subseries *Affines*). It is difficult to estimate the potential number of species in this clade because both these subseries were found to be polyphyletic. All three species have a minute calyx, highly sensitive leaves, grow preferentially on disturbed sites such as roadsides, and have a tendency to become weedy. The group is widespread from tropical South America to Mexico (*M. affinis*). *Mimosa pudica* is introduced and widely naturalized across the tropics.

Clade Q comprises series *Modestae,* except for *M. skinneri*, which was placed in clade R. Species of clade Q grow mainly in northeast Brazil. The only species of series *Modestae* not sampled here is endemic to the Caribbean (*M. viva*), and its placement within clade Q awaits confirmation. All species in this clade have seismonastic leaf movements (Fig. 3c).

Clade R is a large clade (probably 34 species) formed mostly by Cerrado endemics and includes members of Barneby's (1991) subseries *Polycephalae* (20 species), *Dicerastes* (1), *Discobolae* (1), *Hirsutae* (11), and *M. skinneri* (*Modestae*). *Mimosa hirsutissima* and *M. skinneri* extend their ranges beyond the Cerrado, while three other species grow in dry grasslands in Paraguay and Argentina. Like species of clade O, this group also shows diverse fire adaptations, including erect virgate stems arising each year from a xylopodium, and many of them are functionally herbaceous subshrubs. The monotypic subseries *Dicerastes* and *Discobolae* are nested within the clade, confirming their affinities as envisaged by Barneby (1991). Resolution within this clade is very poor. The placement of subseries *Polycephalae*, *Dicerastes*, *Discobolae*, and *Hirsutae* in the same clade seems morphologically plausible given the overall similarities in flowers, indumentum and foliage. However, the inclusion of *M. skinneri* in this group is unexpected and intriguing given its morphological affinites with species of clade Q.

Clade S includes *M. xanthocentra* and *M. verecunda* in subseries *Pudicae* and *M. jacobita*, and probably its putative sibling species in subseries *Bipennatulae*, *M. bipennatula* (not sampled here). All these species are restricted to the Cerrados of Brazil and Bolivia, except *M. xanthocentra*, which has a broader geographic range across South and Central America. All species share a paleaceous-pappiform calyx and almost free filaments.

Clade T is a taxonomically heterogeneous group mostly comprising species of subseries *Mimosa* (all except *M. acapulcensis* and *M. sousae*), but also includes *M. casta* (subseries *Castae*) and *M. tequilana* (subseries *Affines*). The estimated number of species in this clade is nine (seven sampled here), and most of them are widespread across the neotropics, being very common in disturbed sites. The inclusion of *M. tequilana* within this clade is not surprising given its reduced leaf morphology of only one pair of pinnae, each with two pairs of large leaflets, a character shared by most species sampled in this group. One exception is *M. casta*, which has far more leaflets per pinna, but which in everything else resembles *M. velloziana* (subseries *Mimosa*). The Mexican species of subseries *Mimosa*, *M. acapulcensis*, and *M. sousae*, which are morphologically very similar to species in clade T, are placed in the mostly Mexican clade V (see below). This and other examples stress the apparent importance of geography in structuring the phylogeny of *Mimosa*. Although Barneby (1991) placed these species in different subseries, he had doubts on the matter and noted several possible inconsistencies in this group and anticipated the relationships between *M. casta*, *M. tequilana*, and *M. acapulcensis*, as found here.

Clade U combines species from subseries *Pedunculosae* with one of the two varieties of the polyphyletic *M. polycarpa* (subseries *Polycarpae*) sampled here, but as sampling within this group remains very sparse (only two of 10 species of subseries *Pedunculosae*), more species need to be sequenced to properly ascertain the composition of this clade. A link between subseries *Pedunculosae* and *Polycarpae* was already predicted by Barneby (1991). The species of this clade grow in open habitats in Paraguay, Argentina, Bolivia, and southern Brazil.

Clade V comprises subseries *Lactifluae* (excluding *M. incarum*) and also *M. acapulcensis* and *M. sousae* (subseries *Mimosa*). Of a total of 11 potential species in this clade, eight were sampled. The range of the group is mainly in southern Mexico, with one species extending to Central America. The peculiar leaf morphology of *M. acapulcensis* and *M. sousae*, of a single pair of pinnae bearing two large leaflets each, is typical of subseries *Mimosa* (see clade T), suggesting that this characteristic evolved independently in the genus. There is weak support for this essentially Mexican clade as sister to the Andean clade W, a geographical sister group relationship also found for clade C.

Clade W is taxonomically disparate and is better defined by its geographical distribution restricted to the Andes than any obvious morphological or classificatory coherence. This clade combines members of subseries *Bolivianae*, *Pectinatae*, *Polycarpae* (*M. woodii* and *M. loxensis*), and also *M. incarum* (subseries *Lactifluae*) and *M. rusbyana* (subseries *Castae*). Many of them are local endemics, restricted to single inter-Andean dry valleys.

Clade X is a large clade that incorporates series *Myriophyllae* and many of the subseries proposed by Barneby (1991) in section *Mimosa* and also includes the whole of section *Calothamnos*. This clade is largely distributed in southern South America where subtropical climates predominate (Argentina, Uruguay, Paraguay, and southern Brazil) and also in highland areas at lower latitudes. In spite of poor resolution and insufficient taxon sampling in clade X, there are indications that some of Barneby's groups may be monophyletic, such as subseries *Obstrigosae* (clade formed by *M. ramboi*, *M. ramulosa*, and *M. sprengellii*). Furthermore, the possibility that section *Calothamnos* is monophyletic cannot be dismissed, since the relationships between elements of this group were unresolved in the Bayesian analysis. The fact that the parsimony analysis (Appendix S4) suggests that this group is monophyletic is explained by the inclusion of indels in the parsimony analysis that were not included in the Bayesian analysis. An analysis based on plastid and nuclear DNA sequences containing a better taxon sampling of *Calothamnos* supports its monophyletism and provide some internal resolution within this group (Savassi-Coutinho, 2009).